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Eutherian Tarsals from the Late Paleocene of Brazil

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ABSTRACT

Disassociated eutherian proximal tarsals (astragalus, calcaneum) from Riochican (late Paleocene) fissure fills near São José de Itaboraí, Rio de Janeiro, Brazil, are described and, where feasible, are assigned to dental species from that locality, based on predicted morphology, relative size, and relative abundance. Two cingulate xenarthrans are present; one is probably a dasypodid, whereas the other may pertain to the Glyptodontidae. Ankle specializations of *Carodnia vierai* are unlike those of astrapotheres and Dinocerata, but similar to those of *Pyrotherium* and suggest reference to the Pyrotheria; *Tetragonostylops apthomasi* is pedally a primitive astrapothere. Notoungulate tarsals from Itaboraí, referred to *Camargomendesia pristina* (Henricosborniidae) and *Colbertia magellanica* (?Oldfieldthomasiidae), are of generalized aspect within the order, and represent a primitive morphotype from which later notoungulate families diverged. Litoptern tarsals are assigned to three species, *Anisolambda prodromus, Ernestokokenia parayirunhor,* and a new form; astragali and calcanea of "condylarth" aspect are referred to *Lamegoia conodonta, Victorlemoinea prototypica,* and *Ernestokokenia protocenica.* The fact that some dentally primitive taxa (including a supposed congener of a dental and tarsal condylarth) bear the diagnostic litoptern ankle specializations, whereas others, including an advanced and dentally litoptern-like form do not, heightens the problem of distinguishing the two groups as currently recognized, and indicates that the fundamental specializations of the Litopterna are postcranial, not dental. *Victorlemoinea,* heretofore considered a macraucheniid litoptern but probably pertaining to the new family, Sparnotheriodontidae, shares derived pedal characters with the didolodonts; among the didolodonts, *Ernestokokenia protocenica, Lamegoia conodonta,* and ?*Didolodus* sp. seem to form a natural (monophyletic) group definable by tarsal features.

INTRODUCTION

Little is known of the once-diverse but now largely extinct eutherians of South America—currently grouped into some six to nine orders—prior to the ?early Eocene Casamayorian Land Mammal Age. With the exception of one partial skeleton of *Utaetus* (Simpson, 1948), the pre-Deseadan (early Oligocene; Marshall et al., 1977) record of xenarthrans consists only of isolated cingulate scutes. The early record of fossil mammals in South America is almost exclusively Patagonian, and with the exception of a small ?Late Cre-

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taceous faunule from Laguna Umayo, Peru (Grambast et al., 1967) begins with the Riochican Land Mammal Age, presumed to be late Paleocene (Simpson, 1935a; Marshall, Hoffstetter, and Pascual, in press). The Patagonian Riochican localities, grouped into several faunal zones (Simpson, 1935a, 1948), have produced a modest diversity of ungulates represented largely by isolated teeth. The fauna from São José de Itaboraí, Brazil, therefore assumes a position of singular prominence in any treatment of early South American fossil mammals, because it contains the most diverse and best represented assemblage of Riochican vertebrates of any fauna on the continent.

The fossils derive from predominantly argillaceous marls which fill fissures and underground channels in a limestone, the Itaboraí Formation, of probable Late Cretaceous or early Paleocene age (Francisco and Souza Cunha, 1978). The limestone occurs in a small, local tectonic basin in a Precambrian gneissic and granitic basement rock intruded by Early Cretaceous basalts, about 25 km. northeast of Niteroi, State of Rio de Janeiro. The fossils have been recovered during the course of commercial limestone quarrying over the past 35 years.

The mammals of Itaboraí have been described largely by Paula Couto (1952a, 1952b, 1952c, 1952d, 1954) with additions, emendations, and refiguring (1961, 1962, 1963, 1970, 1978a, 1978b, 1978c, 1979). There is some question as to the precise age of the fauna, and it is possible that faunules from the various fissures may not be isochronous. Although the fauna is obviously at ecologic variance with those known from Patagonia (Paula Couto, 1970), Paula Couto (1952a) has assigned the Itaboraí assemblage a Riochican age, based on the presence of *Carodnia,* which occurs in Patagonia only in the earliest faunal zone of that age (Simpson, 1935a). The other genera in common, ?*Nemolestes* (see Marshall, 1978), *Patene, Ernestokokenia, Asmithwoodwardia, Anisolambda,* and *Victorlemoinea,* occur in the Casamayoran or Casamayoran and Riochican of Patagonia.

In addition to the well-represented dentitions described and figured by Paula Couto, the collections from Itaboraí include a wide diversity of well-preserved but (with one exception) unassociated postcranial remains. In the present paper I describe the eutherian proximal tarsal bones (astragalus, calcaneum) and discuss their significance with respect to the phylogeny of the various groups involved. The American Museum of Natural History has a small collection of Itaboraí tarsals, but the bulk of this study is based on the large collections of the Divisão Nacional de Producão Mineral.

Abbreviations for institutions cited in the text: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, N.Y.; ACM, Pratt Museum, Amherst College, Amherst, Mass.; DNPM and DGM, Divisão Nacional de Producão Mineral, Rio de Janeiro, Brazil; MACN, Museo Argentino de Ciencas Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MNRJ, Departamento de Geologia e Mineralogia, Museu Nacional de Rio de Janeiro, Brazil.

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METHODOLOGY

The Itaboraí tarsals are of particular interest but present special problems because of

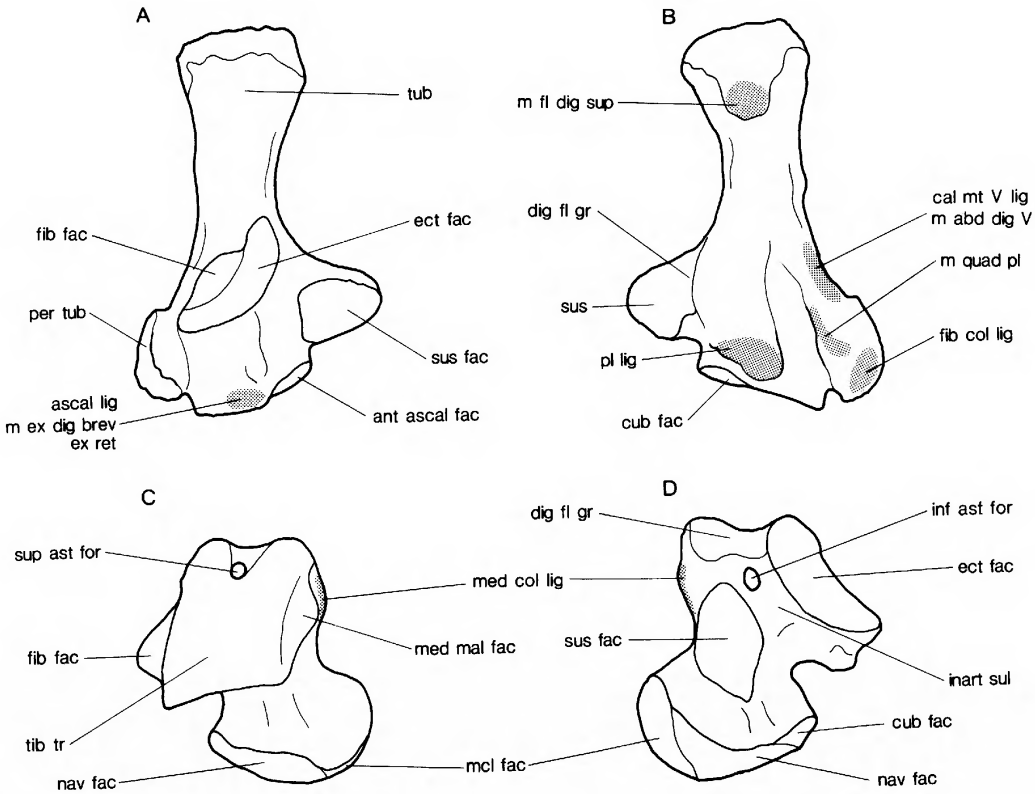

FIG. 1. Right calcaneum (A, B) and astragalus (C, D) of *Arctocyon ferox* (AMNH 16543), in plantar (B, D) and dorsal (A, C) views, illustrating terminology used in this paper. Dot pattern indicates areas of origin/insertion of muscles and ligaments as noted in the text. Abbreviations: ant ascal fac, anterior astragalocalcaneal facet; ascal lig, attachment of astragalocalcaneal ligament; cal mt V lig, attachment of calcaneal metatarsal V ligament; cub fac, cuboid facet; dig fl gr, groove for deep digital flexor tendon(s); ex ret, attachment of extensor retinaculum; ect fac, ectal facet; fib col lig, attachment of fibular (lateral) collateral ligament; fib fac, fibular facet; inart sul, interarticular sulcus; inf ast for, inferior astragalar foramen; mcl fac, facet for the medial collateral ligaments; med mal fac, facet for medial malleolus of tibia; med col lig, attachment of medial (tibial) collateral ligament; m abd dig V, attachment of abductor digiti quinti muscle; m ex dig brev, attachment of extensor digitorum brevis muscle; m fl dig sup, attachment of flexor digitorum superficialis muscle; m quad pl, attachment of quadratus plantae muscle; nav fac, navicular facet; per tub, peroneal tubercle; pl lig, attachment of plantar ligaments (to the cuboid and cuneiforms) and tarsal fibrocartilage; sup ast for, superior astragalar foramen; sus, calcaneal sustentaculum; sus fac, sustentacular facet; tib tr, tibial trochlea; tub, tuber calcis.

their occurrence. The fauna is well known and well represented, and confusing elements such as rodents and primates (which appear in the Deseadan, early Oligocene) are absent. Yet, except for *Carodnia,* all tarsals lack association and a number of members of the fauna (*Asmithwoodwardia scotti,* a new unnamed form, *Ernestokokenia parayirunhor, E. protocenica, Lamegoia conodonta,* and *Tetragonostylops apthomasi*) pertain to dental groups, families, or even orders for which associated postcranial remains are unknown. There can be no predicted morphology for these forms. The establishment of reliable associations is of paramount importance. I have employed three interdependent methods in making the associations proposed below; morphology, relative size, and relative abundance. Associations of astragali to calcanea were based on morphology, relative size and abundance, and "fit."

Work in progress strongly supports the hy-

TABLE 1
Genera of South American Ungulates with Ankles Known by Association[a]

Litopterna
Theosodon (Macraucheniidae)
Proterotherium (Proterotheriidae)
Protheosodon (?Proterotheriidae)[b]
Astrapotheria
Parastrapotherium (Astrapotheriidae)
Astrapotherium (Astrapotheriidae)
Pyrotheria
Pyrotherium (Pyrotheriidae)
Notoungulata
Boreastylops (Notostylopidae)
Thomashuxleya (Isotemnidae)
Adinotherium (Toxodontidae)
Scarrittia (Leontiniidae)
Rhynchippus (Notohippidae)
Homalodotherium (Homalodotheriidae)
Protypotherium (Interatheriidae)
Pachyrukhos (Hegetotheriidae)

[a] The ankle of these is known by direct association.
[b] Simpson (1948, p. 117) doubted the association of hind limb to mandible made by Loomis (1914, p. 41), and guessed that the postcranial elements might pertain to a notoungulate. The ankle in question (ACM 3001) is definitely that of a litoptern, probably a proterotheriid, and I therefore consider Loomis's association to be correct.

pothesis forwarded by Szalay (Szalay and Decker, 1974; Szalay, 1977; see also Schaeffer, 1947; Kielan-Jaworowska, 1977; Novacek, 1980) that tarsals assigned to the Maastrichtian genus *Protungulatum* present with few exceptions the morphology which would be predicted for a primitive eutherian morphotype. Among ungulates, this type of tarsus, with some minor modifications and variations, has a wide distribution among primitive members of families generally grouped in the order Condylarthra, including the Arctocyonidae, Phenacodontidae, anisonchine Periptychidae, and mioclaenine Hyopsodontidae. This morphotype, as exemplified by *Arctocyon,* is used as the basis for comparison in the descriptions given below, and reference should be made to the references cited above concerning specific features of the primitive eutherian tarsus. The terminology employed is modified after Szalay and Decker (1974) and is given in figure 1.

Relevant South American mammals for which the tarsus is known by association and available for study are listed in table 1 (many other far more specialized species were studied but are not listed). Despite the fact that many available species pertain to later, presumably more derived groups, consideration of structural features shared by diverse members of a higher category (i.e., orders Xenarthra, Notoungulata, Litopterna, Astrapotheria, and Pyrotheria) in comparison to a primitive eutherian morphotype allows the distinction of shared, derived characters peculiar to that higher category, thus permitting preliminary allocation of isolated tarsals.

To aid in association of ungulate tarsals by relative size, comparison was made to a number of primitive ungulates for which the ankle is known by direct association. Ten species of condylarths were selected for this purpose, largely on the basis of availability, but also because they represent a similar level of dental and pedal organization to the species in question. Molar size, highly correlated with body size (Kay, 1975; Gingerich, 1977), was approximated by area (maximum length by maximum width) of M_2, and was compared to maximum astragalar length. The logarithmic linear regression of figure 2 indicates that $\log(M_2 \text{ area}) = -.77 + 1.55 \log(\text{astragalar length})$, with the parameters a and b of the equation $Y = a + bX$ estimated mathematically. (A sample of nine fossil tapiroids yielded a log linear regression with similar slope but slightly greater Y-intercept.) The more questionable Itaboraí tarsal phena were compared to dental species from the quarry and associated with them using the condylarth regression as a standard of comparison (fig. 3). The sample size is small with a large margin of variability (see tables 2 and 3), and the Itaboraí collections include a wide variety of growth stages with a very high proportion of juveniles. Nonetheless, this approach does set broad limits on association by size and is more objective than assessment "by eye."

With one exception, the fossils from Itaboraí lack precise collecting information. That exception is fortunately a large and important sample collected by D. Campos and L. Price in 1968, and is known to be from a

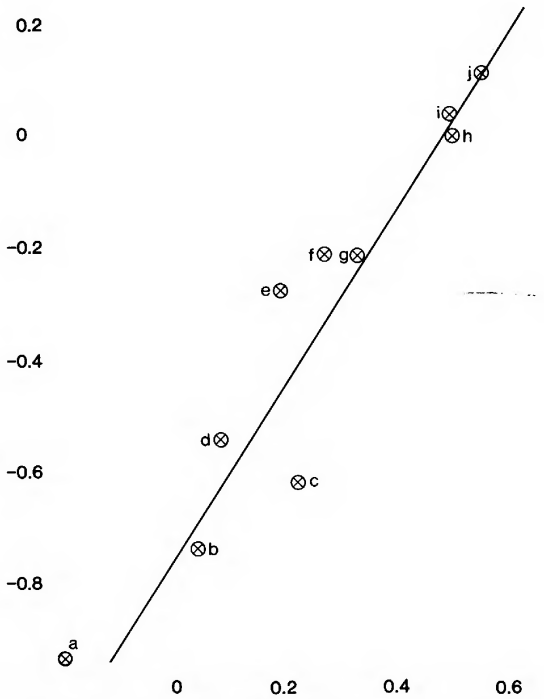

FIG. 2. Logarithmic linear regression of M_2 area (ordinate) *versus* astragalar length (abscissa) of 10 condylarth species. a, *Choeroclaenus turgidunculus*; b, *Anisonchus sectorius*; c, *Chriacus gallinae*; d, *Hyopsodus walcottianus*; e, *Meniscotherium chamense*; f, *Tetraclaenodon puercensis*; g, *Phenacodus wortmani*; h, *Periptychus rhabdodon*; i, *Arctocyon ferox*; j, *Phenacodus primaevus*.

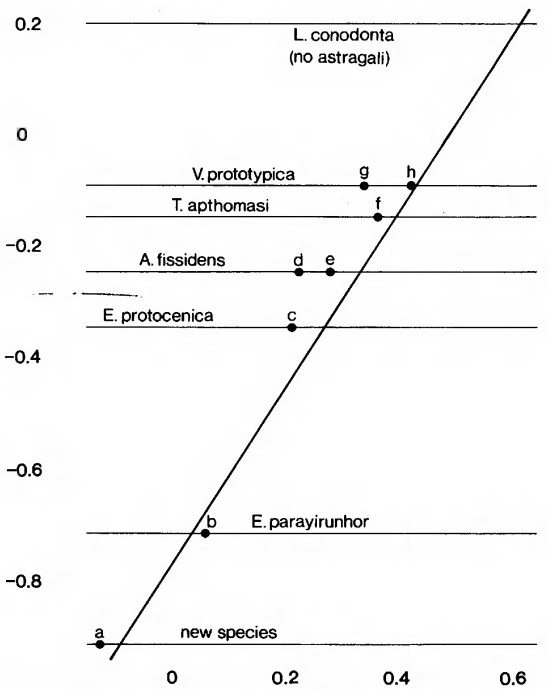

FIG. 3. Logarithmic linear regression of M_2 area (ordinate) *versus* astragalar length (abscissa) of various Itaboraí ungulates, with associations as hypothesized and discussed in the text, using the regression line of figure 2 ($\log(M_2 \text{ area}) = -.77 + 1.55 \log(\text{astragalar length})$) as a standard of reference.

single fissure. The remainder of the specimens, although now stored at the DNPM as they were collected, were picked up by workers and are of uncertain provenience within the quarry. These collections (all at the DNPM; the AMNH material was omitted from this part of the study) were pooled into five additional lots, based on matrix, color, and preservation of the bone, and date collected. The astragali and calcanea from each lot were sorted into morphological and size groups, counted, and measured. The dental remains from each lot were then sorted to species and where feasible were counted. Most of the dental material consists of isolated cheek teeth, and it was not always possible to sort some of the closely similar forms (i.e., among the notoungulates), as many deciduous teeth are present and the locus of certain isolated cheek teeth is difficult to determine. Such samples are pooled and considered in more general terms. The relative abundances of dental and pedal remains are given in tables 4 and 5. Far more reliable relative abundance comparisons would be made on the basis of minimum number of individual counts, as commonly used in archeological faunal analysis (e.g., Chaplin, 1971), but this was not possible for reasons given above.

Pending an urgently needed revision of the Itaboraí fauna, soon to be undertaken in Brazil, such emendations and additions as seem necessary are given below.

RESULTS

NOTES ON THE FAUNA: A revised list of the eutherians from Itaboraí and their distribu-

TABLE 2
Measurements (in Millimeters) of Itaboraí Eutherian M_2s

Species	Length		Width		N
	OR	$\bar{X}$	OR	$\bar{X}$	
Condylarthra					
Asmithwoodwardia scotti	3.5	3.5	2.9–3.1	3.0	3
Ernestokokenia protocenica	8.1	8.1	6.9	6.9	1
Lamegoia conodonta	14.4	14.4	12.0	12.0	1
Victorlemoinea prototypica	11.4	11.4	7.2	7.2	1
Litopterna					
Unnamed	3.8–4.5	4.1	3.2–3.8	3.6	18
Ernestokokenia parayirunhor[a]	4.5–5.7	5.0	4.0–4.5	4.2	16
Anisolambda prodromus[a]	9.4–9.5	9.5	6.0	6.0	2
Notoungulata					
Itaboraitherium atavum	5.1	5.1	3.1	3.1	1
Camargomendesia pristina	4.8–5.6	5.2	3.8–4.7	4.2	12
Colbertia magellanica[a]	5.9–8.0	6.9	4.1–6.0	5.0	17
Astrapotheria					
Tetragonostylops apthomasi[a]	10.2–11.9	11.1	6.7–8.0	7.3	5
?Pyrotheria					
Carodnia vierai[a]	28.8–33.5	31.2	27.2–28.2	27.7	2

[a] From Paula Conto, 1952a, 1952b.

tions among the various lots are given in table 4. *Asmithwoodwardia scotti,* dentally the most primitive known eutherian from South America, was at first referred by Paula Couto (1952a) to the Hyopsodontidae, but later (1978b) transferred to the Didolodontidae, following arguments presented by McKenna (1956). It is the smallest ungulate from the quarry and is extremely rare; aside from the described skull and mandible and five additional specimens in lot 2, only one other specimen, from lot 3, is referred to this species, and that with some doubt. *Ernestokokenia protocenica,* a medium-sized didolodont, also has a limited distribution, occurring only in lots 2 and 3, where it is moderately abundant. Paula Couto (1952a) considered the isolated specimens MNRJ 1841V and 1842V, a right P_4 and left P^4, respectively, as probably representing a new and distinctive member of the Didolodontidae. Comparison with other didolodonts, both from Patagonia and Itaboraí, suggests that these pertain to *Lamegoia conodonta* Paula Couto, 1952a. Additional isolated cheek teeth among the DNPM material may be added to this as yet hypothetical composite. The result is a sharply distinct form with an enormously enlarged P^4 (reminiscent of periptychid condylarths) and the molars greatly enlarged from first to third, but this does not seem improbable and in fact represents enhancement of specialized trends known in other didolodonts such as *Ernestokokenia protocenica. Lamegoia* is a rare form and is also found only in lots 2 and 3. *Victorlemoinea prototypica,* heretofore considered a macraucheniid litoptern (Paula Couto, 1952a, 1978b; see also Simpson, 1948), is tentatively excluded from that family and order, based on pedal evidence presented below. It is a rather rare form also and was found in lots ?1, 2, and 3.

An undescribed species, dentally similar to species generally grouped in the Didolodontidae but here recognized as litoptern because of tarsal specializations, is added to the faunal list. Its full description and detailed comparison with didolodonts and primitive litopterns are in progress. Except for *Asmithwoodwardia scotti,* this is the smallest ungulate from Itaboraí and is the single most

abundant non-notoungulate species. It may seem paradoxical that a species heretofore unrecorded should be represented by so many specimens, but except for two dubious teeth it is known only from the 1968 Campos/Price material, and thus was collected after Paula Couto's initial studies and descriptions. Dentally, it is rather primitive and most comparable to *Ernestokokenia parayirunhor* in this fauna. Both have enlarged lower canines, but the new form is sharply distinct in that the premolars are less molarized (P^4 and P_4 lack the metacone and paraconid, respectively; P_3 is a simple, unicuspid tooth) yet are inflated, bringing to mind a primitive mioclaenine hyopsodontid such as *Ellipsodon*. *Ernestokokenia parayirunhor*, traditionally placed in the Didolodontidae (Paula Couto, 1952a) but here considered litoptern because of the tarsus, is questionably present in the Campos/Price collection, moderately abundant in lots 2 and 3, and very abundant in lots 4 and 5.

Itaboraitherium atavum, a notoungulate referred originally by Paula Couto (1954) to the Patagonian notostylopid genus *Homalostylops* but later (Paula Couto, 1970) placed in the Oldfieldthomasiidae under the new generic name, is very rare and is found only in lot 2 and questionably in lot 3. As currently conceived, the species *Colbertia magellanica* is enormously variable in size and morphology (see Paula Couto, 1952b). Isolated and worn teeth may be confused with *Camargomendesia pristina* (a generally smaller and more primitive species) where both occur because, as noted above, of the difficulty of distinguishing deciduous from adult teeth and of determining tooth locus within the jaw. *Colbertia* is found in all lots except 1 and ?4, and is present in great (uncounted) numbers in lot 3, where *Camargomendesia pristina* probably occurs also. This last species has recently been considered by Paula Couto (1979) to belong to *Othnielmarshia* Ameghino, but the relatively high crowns, reduction of upper molar ectoloph folds, well-developed lower molar entolophid (particularly on M_3), and strongly marked upper molar pattern with at least second crista and crochet, and first crista variably present, seem to oppose reference to the Patagonian genus. *Camargomendesia* is thus provisionally recognized as valid. Nonetheless, it shows no specializations characteristic of other, more derived early notoungulate families, and is therefore retained in the Henricosborniidae.

TABLE 3
Lengths (in Millimeters) of Eutherian Tarsals from Itaboraí

Species	Astragalus OR	Astragalus $\bar{X}$	Astragalus N
Condylarthra			
Asmithwoodwardia scotti	—	—	—
Ernestokokenia protocenica	17.3–17.8	17.6	2
Lamegoia conodonta	—	—	—
Victorlemoinea prototypica	19.5–28.0	22.9	6
Litopterna			
Unnamed	5.5–8.2	7.3	37
Ernestokokenia parayirunhor	11.0–12.2	11.6	15
Anisolambda prodromus	14.3–19.3	16.5	6
Notoungulata			
Itaboraitherium atavum	—	—	—
Camargomendesia pristina	10.0–12.2	10.9	11
Colbertia magellanica	11.0–17.2	13.9	50
Astrapotheria			
Tetragonostylops apthomasi	18.7–23.3	21.0	5
?Pyrotheria			
Carodnia vierai	51.0	51.0	1
Xenarthra			
Dasypodidae, indet.	11.2	11.2	1
?Glyptodontidae, indet.	9.2	9.2	1
	Calcaneum		
Condylarthra			
Asmithwoodwardia scotti	—	—	—
Ernestokokenia protocenica	38.0	38.0	1
Lamegoia conodonta	—	—	—
Victorlemoinea prototypica	43.2–44.0	43.6	2
Litopterna			
Unnamed	13.3–17.1	15.2	26
Ernestokokenia parayirunhor	21.1–23.0	22.0	6
Anisolambda prodromus	—	—	—
Notoungulata			
Itaboraitherium atavum	—	—	—
Camargomendesia pristina	20.4–22.9	21.7	11
Colbertia magellanica	25.7–33.8	29.5	22
Astrapotheria			
Tetragonostylops apthomasi	—	—	—
?Pyrotheria			
Carodnia vierai	—	—	—

TABLE 4
Relative Abundances of Eutherian Dentitions

Species	Lot 1		Lot 2		Lot 3		Lot 4		Lot 5		Lot 6	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Asmithwoodwardia scotti	—	—	6	2	?1	0	—	—	—	—	—	—
Unnamed	344	58	—	—	—	—	—	—	—	—	—	—
Ernestokokenia parayirunhor	?2	0	15	4	41	12	62	78	32	86	—	—
Anisolambda prodromus	34	6	14	4	12	4	3	4	2	5	2	22
Ernestokokenia protocenica	—	—	46	14	11	3	—	—	—	—	—	—
Lamegoia conodonta	—	—	5	2	5	2	—	—	—	—	—	—
Victorlemoinea prototypica	?1	0	18	5	5	2	—	—	—	—	—	—
Itaboraitherium atavum	—	—	?10	3	[a]	—	?2	3	—	—	—	—
Camargomendesia pristina	185	31	?2	1	[a]	—	9	11	—		—	—
Colbertia magellanica	—	—	198	59	[a]	—	—	—	3	8	1	11
Tetragonostylops apthomasi	24	4	?70	21	213	65	4	5	—	—	6	67
Carodnia vierai	—	—	20	6	46	14	—	—	—	—	—	—

[a] Lot 3 contains an enormous number of isolated notoungulate teeth which time did not permit sorting or counting.

Tetragonostylops apthomasi pertains to the Trigonostylopidae, a family given ordinal status by Simpson (1967), but here more conservatively retained in the Astrapotheria. It is found in all lots except 5, and is occasionally (lots 2, 3) very abundant. *Carodnia vierai,* placed in a new and monotypic order, Xenungulata, by Paula Couto (1952a) occurs in modest numbers in lots 2 and 3. (The counts for *Tetragonostylops* and *Carodnia* are relatively inflated because their teeth are so distinct that even fragments are readily recognized.)

The order Xenarthra is known at Itaboraí only from four dasypodid plates collected by Rosendo Pascual and described by Scillato Yane (1976) as *Prostegotherium* aff. *astrifer.* No additional plates were found in the collection, but several postcranial specimens, including astragali of a dasypodid and a ?glyptodontid were encountered. It cannot be determined whether the dasypodid astragalus

TABLE 5
Relative Abundances of Eutherian Tarsals

Species	Lot 1		Lot 2		Lot 3		Lot 4		Lot 5		Lot 6	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Asmithwoodwardia scotti	—	—	—	—	—	—	—	—	—	—	—	—
Unnamed	155	75	—	—	—	—	—	—	—	—	—	—
Ernestokokenia parayirunhor	?5	2	—	—	18	10	7	37	1	50	2	9
Anisolambda prodromus	—	—	—	—	9	5	—	—	—	—	1	4
Ernestokokenia protocenica	—	—	4	24	2	1	—	—	—	—	—	—
Lamegoia conodonta	—	—	—	—	1	1	—	—	—	—	—	—
Victorlemoinea prototypica	2	1	3	18	2	1	—	—	—	—	—	—
Itaboraitherium atavum	—	—	—	—			—	—	—	—	—	—
Camargomendesia pristina	40	19	—	—	141	82	11	58	—	—	—	—
Colbertia magellanica	—	—	—	—					1	50	11	48
Tetragonostylops apthomasi	4	2	6	35	—	—	—	—	—	—	11	48
Carodnia vierai	—	—	4	24	—	—	—	—	—	—	—	—
Dasypodidae, indet.	—	—	—	—	—	—	1	5	—	—	—	—
Glyptodontidae, indet.	—	—	—	—	—	—	—	—	—	—	1	4

TABLE 6
Lengths (in Millimeters) of Figured Specimens

Species/Specimen	Figure	Length
Carodnia vierai		
Calcaneum, DGM 336M	3	91.7[a]
Astragalus, DGM 336M	3	51.2
Tetragonostylops apthomasi		
Calcaneum, AMNH 55384	4	36.8
Astragalus, AMNH 55385	4	23.1
Ernestokokenia parayirunhor		
Calcaneum, AMNH 55396	5	21.2
Astragalus, AMNH 55394	5	12.2
Ernestokokenia protocenica		
Calcaneum, AMNH 55390	7	37.8
Astragalus, DNPM LE443	6	17.3
?*Victorlemoinea prototypica*		
Calcaneum, DGM 890M	7	43.5
Astragalus, AMNH 55393	6	27.9
?*Lamegoia conodonta*		
Calcaneium, AMNH 55389	7	45.2
Colbertia magellanica		
Calcaneum, DNPM LE446B	8	27.2
Astragalus, AMNH 55373	8	16.9
Dasypodidae, indet.		
Astragalus, DNPM LE449B	9	10.1
?Glyptodontidae, indet.		
Astragalus, DNPM LE449A	9	9.0

[a] After restoration.

pertains to the species for which plates have been described.

TARSAL DESCRIPTIONS

Carodnia vierai (?Pyrotheria)

Figure 4

DGM 335M includes a left astragalus and the partial skeleton DGM 336M includes a left astragalus and right and left calcanea of this species. The astragalus was described briefly by Paula Couto (1952a). The body is subquadrate and is much deeper medially than laterally. The tibial trochlea presents a nearly flat surface mediolaterally and is broadly convex anteroposteriorly. Unlike *Arctocyon,* the tibial trochlea is subparallel with rather than oblique to the long axis of

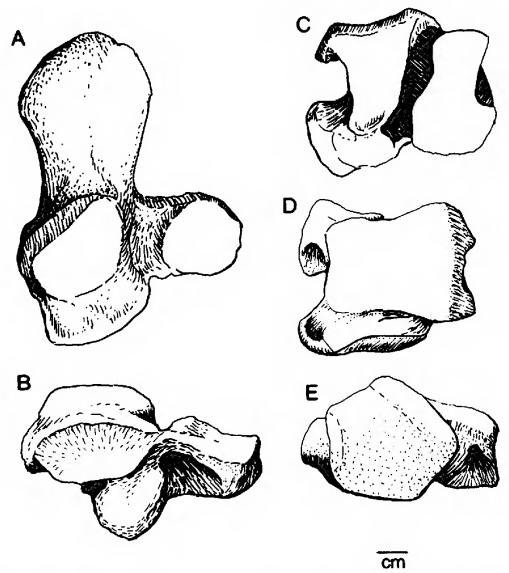

FIG. 4. Left astragalus and right calcaneum (DGM 336M) of *Carodnia vierai,* partially restored. Left column, calcaneum in dorsal (A) and distal (B) views; right column, astragalus in plantar (C), dorsal (D), and distal (E) views. Measurements given in table 3C.

the astragalus, so that rotation at the crurotarsal joint would have been more strictly orthal with respect to the midtarsal joint than it is primitively. The superior astragalar foramen is absent, but a deep notch at the back of the tibial trochlea is continuous with the posteriorly expanded interarticular sulcus on the inferior side of the bone, suggesting the course of the nerve(s) or vessel(s) which traversed this region. There is no separate groove for the digital flexor tendons. Both lateral and medial borders of the tibial trochlea are sharply defined. The articular facet for the fibula is at a high angle to the tibial trochlea and extends the entire anteroposterior length of the body, as in *Arctocyon,* but is outwardly convex, unlike the condition in that genus. Anteriorly, the fibular shelf is absent and the facet occupies the dorsal half of the lateral body wall. Posteriorly, the fibular facet extends to the base of the body and is therefore continuous with the posterolateral portion of the ectal facet. Although direct evidence is lacking (this region is not well preserved on the calcaneum), this implies that a

modified, proboscidean type of calcaneofibular contact was present, at least posteriorly. In graviportal astrapotheres and uintatheres where calcaneofibular contact is known to be lacking, the fibular facet on the astragalus does not extend so clearly to the base of the bone joining the ectal facet. The medial wall of the astragalus also presents a high angle to the tibial trochlea. The head and posterior portion of the astragalar body are extended medially. This, together with the fact that the low, unextended tibial trochlea describes a relatively narrow arc, indicates that the range of extension and flexion at the crurotarsal joint was somewhat limited.

The astragalar neck is extremely short and broad, extending over most of the width of the body. The distal surface is tremendously expanded dorsoventrally, especially on the medial side. The navicular facet occupies nearly the entire distal surface of the head and is very flat. The slight curvature of convexity forms a very low angle with respect to the tibial trochlea, and this, together with the flat, non-oblique and subparallel astragalocalcaneal facets, indicates that oblique rotation at the midtarsal joint and therefore capability of eversion and inversion were limited or absent. A small facet for the short medial collateral ligaments is well defined, and forms a sharp angle with the navicular facet on the medial side of the head.[2] A cuboid facet appears to be lacking from the astragalar head (there is a slight change in curvature medially on the head of DGM 336M, but the head is broken and somewhat distorted.[3] Articulation with the calcaneum indicates the astragalonavicular articulation to have been distal to that of the calcaneum and cuboid, so that astragalocuboid contact, if present, would have been oriented at a high angle to the head of the astragalus. Since no such facet is present, it seems probable that an astragalocuboid articulation was absent (serial tarsus). On the ventral side of the astragalus, the sustentacular and ectal facets are elongate, broad, parallel, and nearly flat. They are separated by a deep interarticular sulcus. The sustentacular facet extends posteriorly from the navicular facet, with which it shares broad contact, and is somewhat concave at its posterior extremity, where articulation on the calcaneum continued somewhat onto the posterior border of the sustentacular shelf. The posteromedial angle of the astragalus is expanded into a prominent knob, probably for the attachment of hypertrophied medial collateral ligaments, which extend to the distal end of the tibia as well as the distal tarsals, and thus aid in lateral stability at the crurotarsal joint.

The poorly preserved calcaneum is short and robust. Little detail is discernible in the articular region on the dorsal surface of the body. The ectal prominence is nearly flat, on a level with that of the sustentaculum, and laterally slopes abruptly inferiad. This probably corresponds to the modified fibular facet, as noted above. The sustentacular facet is flat and does not extend onto the calcaneal neck to reach the cuboid facet. The neck of the calcaneum (that portion distal to the astragalocuboid articulations) is relatively short. On the lateral surface of the calcaneum the peroneal tubercle, to which portions of the lateral collateral ligaments and quadratus plantae muscle attached, is well marked. A ridge extending posteroinferiorly from this indicates the attachment of the calcaneal metatarsal V ligament and possibly the abductor digiti quinti muscle. The distal end of the calcaneum bears a relatively small, dorsoventrally compressed, somewhat medioinferiorly facing cuboid facet. Inferior and somewhat medial to the cuboid facet is a large, rugose prominence. This would have given origin to plantar ligaments attaching to the cuboid, cuneiforms, and tarsal fibrocartilage, which forms the deep surface of the canalis tarsi containing the digital flexor tendons.

[2] This is the "spring ligament" (see Camp and Smith, 1942) facet of Szalay and Decker, 1974. When well defined (with a correspondingly well-developed area for origin of the short medial collateral ligaments on the astragalus), it is often associated with a meniscus or sesamoidal ossification in the ligament. This ossification is often termed the "tibiale" (Matthew, 1937), but as Schaeffer (1947) noted, homology with the reptilian element has not been established and is improbable.

[3] Paula Couto (1952a, p. 386) supposed that a cuboid facet was present on the astragalar head of *Carodnia*, but the feature he describes is medially placed and must be for the medial collateral ligaments. The cuboid borders the astragalus on its lateral side.

Tetragonostylops apthomasi
(Astrapotheria)
Figure 5

These astragali and calcanea are assigned to *Tetragonostylops apthomasi* because they are of appropriate size (fig. 3) and because they are abundant where teeth of this species are abundant (tables 4 and 5). *Tetragonostylops* tarsals are conspicuously absent from lot 3, where numerous dental remains of it occur. Perhaps the five AMNH specimens were culled from this lot, as preservation and coloration of the bone is similar.

The astragalar body is low and subquadrate. The tibial trochlea, very slightly concave in its center, has a relatively low anteroposterior curvature, indicating a modest arc of flexion-extension at the crurotarsal joint. A prominent superior astragalar foramen is present and a widening groove extends posteromedially from it, dividing the tibial trochlea and terminating in a well-marked groove for tendons of the deep digital flexor muscle. A groove for these flexor tendons is seen also on the medial side of the calcaneal body, inferior and just proximal to the sustentaculum. The fibular border of the tibial trochlea is sharply defined and is somewhat higher than the medial border. The facet for the fibula, not quite vertical, occupies the entire lateral side of the astragalar body and slopes onto a very prominent fibular shelf. Juvenile astragali (determined by their smaller size, incomplete fusion of the head to neck, and more porous bone) indicate that development of this shelf occurs ontogenetically, as it is little marked in young individuals. The tibial trochlea extends up the neck of the astragalus. The medial crest of the tibial trochlea is ill-defined and slopes medially into an extensive facet for the medial malleolus of the tibia, indicating an increased weight supporting area for the tibia. Inferior to the medial malleolar facet, the body of the astragalus projects mediad. From below, this projection is seen as a rugose, sweeping crest that extends nearly the entire length of the astragalus. It is evident that, as in *Carodnia,* the short medial collateral ligaments were very well developed.

The astragalar neck is short; the head is dorsoventrally expanded but somewhat narrow mediolaterally, and bears three distinct facets. The medial facet, for the medial collateral ligaments, is large and convexity along its major axis is vertical. The navicular facet is rather flat and its major convexity (implied direction of movement) forms a relatively low angle with respect to the tibial trochlea. The navicular facet is continuous laterally with the cuboid facet, which is large and well defined (alternating tarsus), and inferiorly with the sustentacular facet. The sustentacular facet is large; posteriorly, it is nearly on the same plane as the digital flexor groove, so that, in contrast with *Arctocyon,* there was little "overhang" and consequent articulation with the posterior margin of the calcaneal sustentaculum. The ectal facet is broad, moderately concave, and faces more strictly inferiorly than in *Arctocyon,* in which it faces somewhat laterally. Anteriorly, a secondary facet continuous with the ectal is developed on the anterior face of the fibular shelf and lateral wall of the astragalar body. This unusual articulation, seen also in *Astraponotus,* corresponds to a facet on the dorsal surface

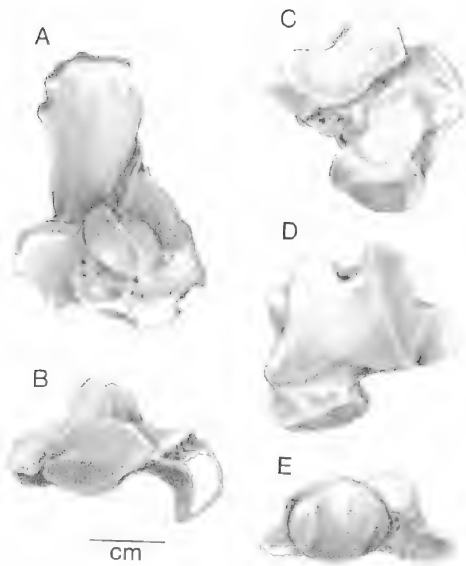

FIG. 5. Left astragalus (AMNH 55385) and calcaneum (AMNH 55384) of *Tetragonostylops apthomasi.* Left column, calcaneum in dorsal (A) and distal (B) views; right column, astragalus in plantar (C), dorsal (D), and distal (E) views. Measurements given in table 6.

of the calcaneal neck, adjoining the cuboid facet. This locking mechanism would appear to have limited the possibility of pedal inversion at the midtarsal joint.

No complete calcanea are available, but judged from AMNH 55384, which has the dorsal portion of the tuber preserved, it was short and very robust. The astragalocalcaneal articulations are placed relatively far forward. The most obvious feature of the calcaneum is the enormous development of the peroneal tubercle into a massive, rugose, inferiorly directed shelf. The short fibular collateral ligaments and the mm. quadratus plantae and extensor digitorum brevis (tarsal head of the flexor digitorum profundus) must have been strongly developed, indicating a reduced capacity for pedal inversion but powerful flexion capability of the ungual phalanges. Anterolaterally on the peroneal shelf a well-marked groove for the m. abductor digiti quinti is present.

The calcaneal ectal facet is mildly convex and short. Unlike *Arctocyon,* it is rather vertically oriented with respect to the body of the calcaneum; distally it faces nearly directly anteriad, whereas its proximal portion faces nearly mediad. It is continuous with the well-defined fibular facet, which is oriented at about 45 degrees to the body of the calcaneum and is strongly convex about both major and minor axes. The calcaneal sustentaculum is short and bears a facet which is oriented anterodorsally. The sustentacular facet achieves broad contact with the cuboid facet. This latter is nearly vertical and has only a slight mediolateral concavity and medial orientation, again indicating a poor ability to invert and evert the tarsus. The inferior part of the tuber calcis, where the superficial digital flexor takes partial insertion, appears to have been strongly projecting. The distal inferior protuberance for origin of calcaneotarsal and tarsal fibrocartilage ligaments is very poorly developed.

LITOPTERNA
Figure 6

As with other advanced ungulate orders, litoptern proximal tarsals are readily recognized as such and cannot be confused with those of any other order of mammals, although certain aspects of the morphology are strikingly similar to artiodactyls, rodents, and rabbits.

Comparison of proterotheriid and macraucheniid tarsals known by direct association with a hypothesized primitive morphotype as exemplified by *Arctocyon* indicates the following features of the astragalus and calcaneum to be derived for the Litopterna: astragalar body spool-like, lacking the superior astragalar foramen, with salient, subequal tibial and fibular crests, and with trochlea extending far posteroinferiorly (digital flexor groove not distinct); astragalar head more or less semicylindrical, with major axis subparallel to that of the tibial trochlea; navicular facet extending onto superior and inferior surfaces of the head, cuboid and medial collateral ligament facets lacking; astragalar sustentacular facet anteroposteriorly elongate, ectal facet deeply concave and with pronounced outward orientation; neck of calcaneum elongate, with strongly oblique calcaneocuboid facet; sustentacular facet of calcaneum anteroposteriorly concave and following same curvature as anterior part of ectal facet.

Although this composite morphology is based primarily on Santacrucian (early Miocene) forms, it is shared by several Itaboraí species. The Itaboraí litoptern tarsals are all very similar and fall into three or perhaps more size categories. The smallest tarsals are entirely restricted to the 1968 collection, where they are found in great abundance (table 5). This distribution coincides with that of dental remains of the unnamed condylarth-like species, also extremely abundant in lot 1 and not surely found elsewhere. Figure 3 indicates further that these tarsals are of appropriate size for the dental material and, moreover, that they are too small to pertain to any other known dental taxon from Itaboraí, except for the very small and rare *Asmithwoodwardia scotti,* which is restricted to lot 2 and possibly lot 3. Slightly larger litoptern tarsals, found in most samples but particularly abundant in lots 3 and 4, are of appropriate distribution and size only for *Ernestokokenia parayirunhor,* which is dentally very close to the above species.

There is some uncertainty as to the referral of the larger litoptern tarsals. These are very

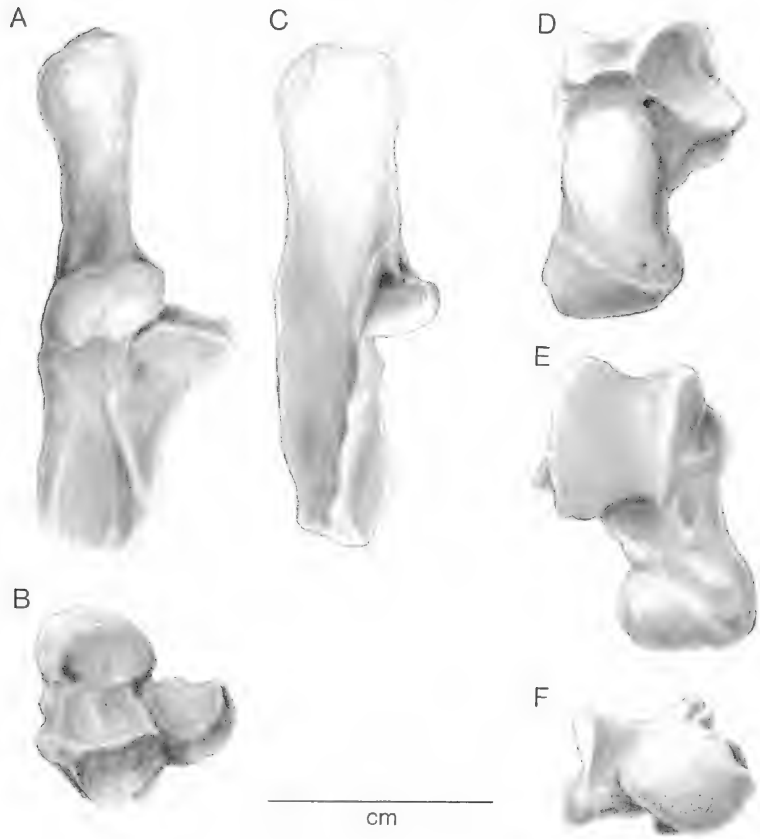

FIG. 6. Right calcaneum (AMNH 55396) and astragalus (AMNH 55394) of *Ernestokokenia parayirunhor.* Calcaneum shown in dorsal (A), distal (B), and lateral (C) views; astragalus shown in plantar (D), dorsal (E), and distal (F) views. Measurements given in table 6.

rare, generally fragmentary, and quite variable in size (table 3). They could represent either more than one species or one variable species, with the sample including juveniles. To assess these possibilities, the size range of the large tarsals was compared to that of the smallest litoptern, which may be assumed to be a single species and for which a large sample is available. To obtain a comparable measurement of size, astragalar length of the fragmentary large specimens was estimated by multiplication of neck width or body width by constants averaged from complete specimens. (Isometry is assumed: logarithmic regression is impractical because of the small number of complete specimens. The difference between the two methods is relatively slight unless the size discrepancies are large.) To account for differences in size, the natural log of the observed size range in each sample was calculated and divided by the sample mean (an otherwise preferable basis of comparison, standard deviation, was not used because the sample of large astragali is very small). The natural log of OR/X in the small species including juveniles is .163, and that of the large astragali is .130; it is therefore possible that only one species is represented, the sample including immature individuals. As shown in figure 3, the log mean astragalar length of this sample (including presumed juveniles), .2175, is most appropriate for *Ernestokokenia protocenica,* but the log mean of the two largest astragali is appropriate for either *E. protocenica* or *Anisolambda prodromus.* These tarsals are referred to *A. prodromus* on the following grounds:

(1) They are of appropriate size, if the sam-

ple represents one species and the fact that some specimens represent juveniles is taken into account.

(2) They pertain to a litoptern, and *Anisolambda* dentally appears to belong within that group, whereas *E. protocenica* may or may not.

(3) *E. protocenica* is absent from lot 6, where *Anisolambda* and a large astragalus occur.

(4) "Condylarth" tarsals, averaging somewhat smaller than the largest of these, are also known and are of appropriate size for *E. protocenica.*

Each of these points considered individually is open to question. Nonetheless, referral of the largest litoptern tarsals to one species, *A. prodromus,* does accord best with the evidence at hand.

The known litoptern tarsals from Itaboraí are thus assigned to three species: the undescribed form, *Ernestokokenia parayirunhor,* and *Anisolambda prodromus.* As with the notoungulates, the tarsals are virtually identical except for size, and the described and figured morphology is that of *E. parayirunhor,* with variations of the other forms as noted.

The astragalar body is spool-shaped, with a deep tibial trochlea sloping upward medially and laterally into salient, parallel, subequal crests. The superior astragalar foramen is absent. The medial crest, curved into a slightly tighter arc than the fibular, is interrupted anteriorly by a clearly defined groove coursing obliquely across it. The biological significance of this structure is unknown (possibly it marks the attachment of an extensor retinaculum); it is absent in the Santacrucian genus *Thoatherium* and faint to absent in the Deseadan genus *Protheosodon.* The medial wall of the astragalar body is flat, and the proximal and distal ends of the medial malleolar facet flare inward inferiorly, clearly defining the extent of the articular surface. The lateral wall of the astragalar body, also nearly vertical, is occupied by a broad fibular facet. The fibular shelf is prominent and is distinctive in being nearly horizontal. Posteriorly, the articular surface for the tibia extends inferiorly to a considerable distance on both medial and lateral crests, and the distinction between it and the groove for the digital flexor tendons is difficult to make. The astragalar neck is relatively long. The head, relatively narrower in the smaller forms than in *A. prodromus,* presents nearly in a straight line with respect to the astragalar body and neck, rather than obliquely as in *Arctocyon.* Cuboid and medial collateral ligament facets are lacking. The shape of the navicular facet describes an acute cone (i.e., is subcylindrical), with the base or large diameter placed laterally, and is considerably expanded onto the neck, both dorsally (lateral) and inferiorly (medial). The axis of rotation appears to be nearly parallel to that at the crurotarsal joint. On the dorsal surface of the neck a variably developed ridge, lacking in the smallest species, is present proximal to the navicular facet. The polished surface of this ridge indicates that the navicular contacted it during hyperextension at the midtarsal joint. The astragalar sustentacular facet is elongate and anteriorly curves up the lateral side of the neck to the head. The ectal facet, well separated from the sustentacular by the interarticular sulcus, is very oblique and deeply concave.

The astragalocalcaneal facets on the calcaneum are located rather far posteriorly (most notably in the small species), so that the neck and tuber are of approximately equal length. The ectal facet is strongly convex; anteriorly, it faces mediodistally whereas posteriorly it faces medioproximally. The ectal facet variably extends also onto the adjacent part of the calcaneal body. The fibular facet is well developed, somewhat oblique to the long axis of the calcaneum, and strongly convex anteroposteriorly but relatively flat transversely. It extends anteriorly to the base of the ectal prominence at its junction with the neck, unlike *Arctocyon.* The neck anterior to the ectal protuberance is relatively flat and is defined medially by a salient ridge, to which the extensor retinaculum, extensor digitorum brevis muscle, and astragalocalcaneal ligament may have attached. The "beak" faintly developed in *Arctocyon* and prominent in the South American condylarths described below is lacking. Medially, the sustentacular shelf and facet are somewhat extended anteroposteriorly. The sustentacular facet is angled and convex, so that it follows nearly the same curvature as the anterior part of the ectal facet, although this is not nearly so well shown as in later litopterns. A narrow articular strip

runs anterodorsally from the sustentacular facet to the dorsomedial angle of the cuboid facet at the end of the calcaneum. The cuboid facet is L-shaped, very markedly oblique, and concave, facing anteromedially. It is bordered laterally by a moderately developed peroneal tubercle, which distally carries an ill-defined groove for the abductor digiti quinti muscle and which continues proximally to about the level of the posterior margin of the ectal protuberance. On the inferior surface of the neck, the prominence for the calcaneotarsal ligaments is weakly developed and continues proximomedially as a ridge along the anteroinferior margin of the sustentaculum.

Ernestokokenia protocenica
(Condylarthra)
Figures 7, 8

This species is dentally rather rare, occurring only in lots 2 and 3, and is moderately abundant only in the latter of these. As noted elsewhere, it is possible that tarsals here ascribed to *Anisolambda prodromus* actually pertain to *E. protocenica.* There is at present no means to resolve this problem definitively, but the tarsals described below are attributed to *E. protocenica* because, as with the teeth, they are rarer than remains of *A. prodromus* and are slightly smaller than tarsals ascribed to that species, and because the dentition of *E. protocenica* is rather primitive, whereas that of *A. prodromus* is more demonstrably litoptern in character (Paula Couto, 1952a: see also Simpson, 1948). It should be noted also that these two tarsal morphs are appropriate in size and morphology only for the two mentioned species among Itaboraí dental taxa. The possibility remains that one or both of the tarsal categories pertain(s) to (a) species unknown dentally and therefore that tarsals of either or both of these species are also as yet unknown, but this does seem really unlikely.

The astragalar body is relatively deep and bears a moderately grooved tibial trochlea with well-defined medial and lateral crests. The astragalar foramen persits in one smaller and presumably juvenile specimen, but is filled with cancellous bone and virtually obliterated in a larger specimen. The medial

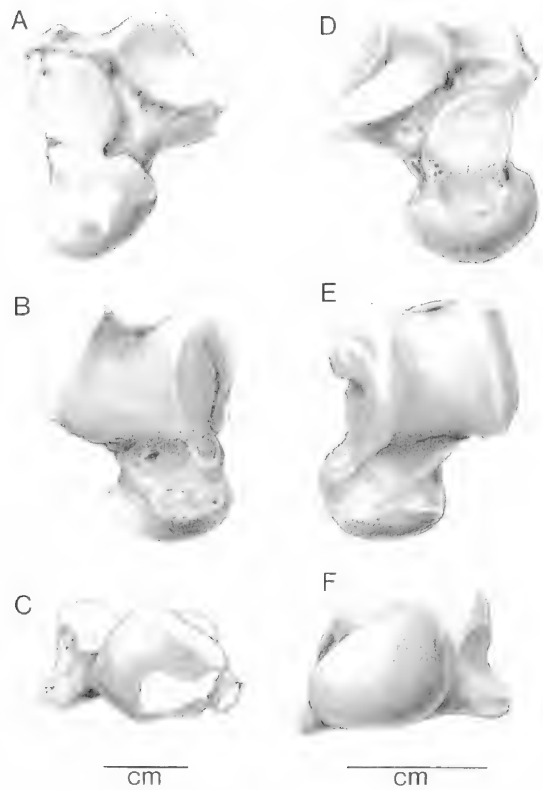

FIG. 7. Right astragalus of ?*Victorlemoinea prototypica* (AMNH 55393; A, B, C) and left astragalus of *Ernestokokenia protocenica* (DNPM LE443: D, E, F), in plantar (A, D), dorsal (B, E), and distal (C, F) views. Measurements given in table 6.

malleolar facet extends far anteriorly onto the neck and nearly to the head of the astragalus, where it curves abruptly mediad. The lateral wall of the astragalar body, also vertical, is covered by an extensive fibular facet that terminates anteroinferiorly in a well-developed fibular shelf. The head is relatively somewhat narrower transversely but is deeper than in *Arctocyon,* and bears a navicular facet that is obliquely oriented, as in that genus. Medial collateral ligament and cuboid facets are absent. A small supplementary facet continuous with that for the navicular but not with the sustentacular is present, and in life contacted the dorsolateral neck of the calcaneum, as articulation of the two tarsals demonstrates. The sustentacular facet is expanded distally and is broadly continuous with the navicular

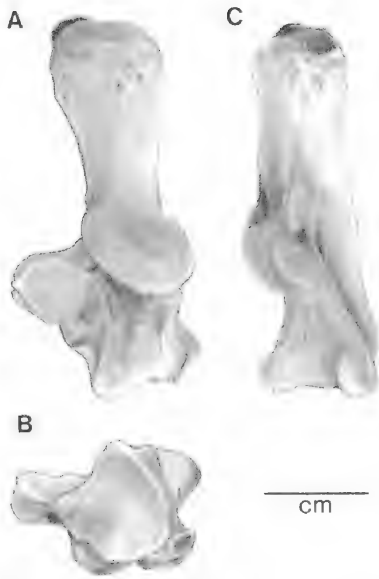

FIG. 8. Left calcaneum of *Ernestokokenia protocenica* (AMNH 55390) in dorsal (A), distal (B), and lateral (C) views. Measurements given in table 6.

FIG. 9. Right calcaneum of ?*Victorlemoinea prototypica* (DGM 890M) in lateral (A), dorsal (B), and distal (C) views. Measurements given in table 6.

facet. The interarticular sulcus is deep and the ectal facet is approximately as in *Arctocyon* in size and orientation. Posteriorly, the groove for the digital flexor tendons is well marked and is somewhat offset from that of the posteroinferior margin of the tibial trochlea, as in *Arctocyon.*

The ectal protuberance on the dorsal surface of the calcaneum is prominent and is situated farther posteriorly on the body than in *Arctocyon.* The articular surface for the fibula is well developed and strongly convex anteroposteriorly but relatively flat transversely; an extensive articular surface is also developed on the lateral surface of the protuberance. The calcaneal ectal facet is broad and obliquely oriented with respect to the tuber, about as in *Arctocyon.* The sustentaculum bears a rather small, ovoid facet which does not attain contact with the cuboid facet at the end of the calcaneum. At its anterior extremity, the calcaneum presents a very salient dorsally projecting beak. The dorsal surface of this prominence is rugose, and probably gave origin to the distal extensor retinaculum and the anterior astragalocalcaneal ligament. A narrow articular surface for the lateral side of the astragalar head descends from the apex of the prominence down its medial surface. The cuboid facet is dorsoventrally elongate and somewhat concave in that direction. Its major axis, following the curvature of concavity, is oblique; the facet is transversely narrowed because, unlike *Arctocyon,* the articular surface does not extend to the inferomedial angle of the calcaneal head. Inferior to the cuboid facet, the tubercle for attachment of the calcaneotarsal and tarsal fibrocartilage ligaments is modestly developed. On the distolateral surface of the calcaneum the peroneal tubercle is robust but not large; the crest extending proximally from it terminates at the base of the ectal prominence rather than passing inferior to it as in *Arctocyon.*

?*Victorlemoinea prototypica*
(Condylarthra)
Figures 7, 9

In addition to the tarsals described above, the Itaboraí collections include an enigmatic assortment of relatively large ungulate astragali and calcanea which cannot be assigned to known species without some (not great)

doubt. The remaining dental species for which tarsals have not been assigned, *Victorlemoinea prototypica* and *Lamegoia conodonta,* are large and correspondingly rare ungulates. There are no known litoptern tarsals, even those of a juvenile, large enough to pertain to either species. These large tarsals are rare, poorly preserved, and quite variable in size and morphology, and in the present lack of a large sample they cannot even be sorted with absolute confidence into phena representing the corresponding biological species: the two morphs described here are valid and quite distinct from each other, but it is possible that another species, unknown dentally, is included in the sample of tarsals referred to *Victorlemoinea prototypica.* It does seem virtually certain, however, that one, or more likely both, of the species *V. prototypica* and *L. conodonta* are included in the two categories presented.

The astragali grouped under the species *V. prototypica* vary enormously in size and morphology; nonetheless, in all basic and important features they are similar, and from the series available, most differences appear to be size related—presumably reflecting ontogenetic changes in proportions—or are due to differences in preservation. The observed size range (adjusted) in a sample of six astragali, calculated as a natural log, is .163, exactly that of the smallest Itaboraí litoptern species, and it is therefore reasonable that a single species is represented. The log mean length of these six specimens is somewhat less than the predicted value for *V. prototypica* (fig. 3), but the largest is very close to that value.

The astragalar body is of comparable depth to that of *Arctocyon.* The tibial trochlea is very shallow, is posteriorly interrupted by an unreduced superior astragalar foramen, and is bordered by sharp lateral and rounded medial crests. The medial wall is relatively vertical, and the facet for the medial malleolus of the tibia is broad and extends well up the neck (nearly to the head in juvenile specimens) of the astragalus. The fibular facet on the lateral side of the astragalus is extensive and vertical, and a prominent fibular shelf is developed anteroinferiorly. The neck is moderately long. The head is transversely narrow but deep, both medially and laterally, and

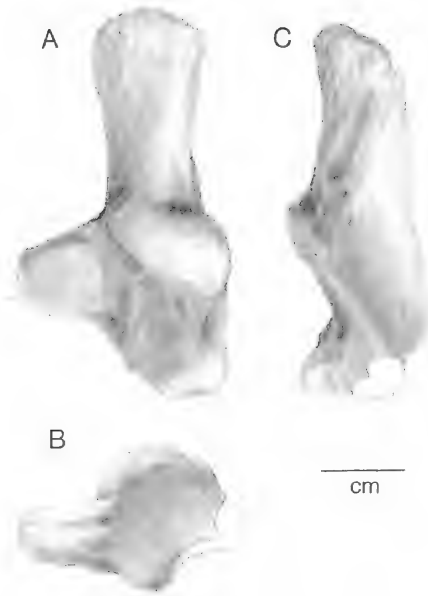

FIG. 10. Left calcaneum of ?*Lamegoia conodonta* (AMNH 55389) in dorsal (A), distal (B), and lateral (C) views. Measurements given in table 6.

bears three facets. The medial collateral ligament facet is very broad, dorsoventrally and proximodistally convex, and meets the navicular facet at a relatively high angle. The navicular facet, restricted to the median portion of the head, is oriented much more vertically with respect to the astragalar body than in *Arctocyon.* The cuboid facet, occupying the inferolateral portion of the head, is broadly continuous posteroinferiorly with the sustentacular facet. Part of this facet was for contact with the neck and medial side of the calcaneal neck, but articulation of appropriately sized astragali and calcanea indicates that astragalocuboid contact was also well developed (alternating tarsus). The sustentacular facet is anteroposteriorly elongate and, as noted, achieves very broad contact with the navicular facet. The astragalar ectal facet is somewhat transversely broader than in *Arctocyon,* but its moderate convexity and outward presentation are as in that form. The ectal and sustentacular facets are separated by a deep interarticular sulcus. The groove for the digital flexor tendons at the posteroinferior margin of the astragalus is broad and sharply distinct.

The ectal protuberance of the calcaneum

is similar to that of *Arctocyon*; the calcaneal ectal facet is broadly convex anteroposteriorly and faces anteromedially. The fibular facet is transversely broad and well developed. The sustentacular shelf is relatively deep; the sustentacular facet extends anteriorly to achieve broad contact with the calcaneal cuboid contact. As in *Ernestokokenia protocenica,* the anterodorsal portion of the calcaneal neck is prolonged dorsally into a distinct protuberance; the cuboid facet, extending up the distal face of this eminence, is also very similar to that of *E. protocenica* except that it extends medially also, forming an inverted V-shape. The tuberosity inferior to the cuboid facet, for attachment of the calcaneotarsal and tarsal fibrocartilage ligaments, is modestly developed. The peroneal tubercle is rather enlarged and rugose, suggesting well-developed lateral collateral ligaments and the quadratus plantae muscle.

?*Lamegoia conodonta*
(Condylarthra)
Figure 10

Tarsals ascribed to *Lamegoia conodonta* are the rarest among Itaboraí ungulates: one astragalus from DNPM lot 3 and one calcaneum in the AMNH collections are referred here. The astragalus (not figured) is very poorly preserved and no measurements could be reliably estimated, although it is as large as the largest referred to ?*Victorlemoinea prototypica,* above. This is less than the expected size of *L. conodonta* (fig. 2B), unless the specimen pertains to a juvenile. In preserved morphology, it is very similar to that of *E. protocenica* and to an unassociated specimen in the AMNH collection of ?*Didolodus* from the Casamayoran of Chubut (Colhué-Huapí). The body bears a moderately deep tibial trochlea with well-defined and subequal but rounded medial and lateral crests. It cannot be determined whether an astragalar foramen was present. As far as can be determined the medial and lateral walls of the body are vertical; medially, the facet for the medial malleolus of the tibia is well developed and extends anteriorly onto the neck where it flares sharply mediad, as in *E. protocenica.* The head is broad and deep, being nearly the size of the body, and is somewhat rotated dorsomedially, as in *Arctocyon.* The astragalar sustentacular facet is small and rounded, and does not attain contact anteriorly with the articular surface(s) of the head. A cuboid facet is probably lacking.

The calcaneum certainly pertains to a juvenile because the epiphysis of the tuber calcis is unfused and lacking; nonetheless, the specimen is comparable in size to adult calcanea referred above to ?*Victorlemoinea prototypica.* The bone is porous and eroded, as is common in immature tarsals, but in known features it is similar to that of *E. protocenica.* The calcaneal ectal facet bears a similar orientation and placement to that of *Arctocyon,* but is somewhat less convex; the region of the fibular facet is eroded, but contact between these two elements appears to have been present. The sustentaculum is moderate in depth, unlike that ascribed to ?*V. prototypica,* and bears a relatively small, round facet which does not extend to the cuboid articulation (reflected in the isolated nature of the astragalar sustentacular facet, as described above). The dorsal surface of the calcaneal neck, as in *E. protocenica* and ?*V. prototypica,* is prolonged into a conspicuous beak (a supplementary facet for the astragalus is present on its medial border); the cuboid facet occupies its distal surface and is thus dorsoventrally expanded. As in *E. protocenica,* this articular surface does not occupy the inferomedial angle of the calcaneal head. Inferiorly, the protuberance for attachment of calcaneotarsal and tarsal fibrocartilage ligaments is modestly developed. The peroneal tubercle on the distolateral corner of the calcaneum is robust but modestly developed and extends posterosuperiorly to join the base of the fibular side of the ectal protuberance, as in *E. protocenica* but unlike *Arctocyon* and all other forms considered here.

NOTOUNGULATA
Figure 11

Isolated notoungulate astragali from the Early Tertiary of South America are readily recognized as such but are not easily identified as to genus or even family. Judged from comparison of representatives of all notoungulate families (for which the tarsus is known) with a hypothetical primitive ungulate mor-

photype as exemplified by *Protungulatum* or *Arctocyon,* the notoungulate proximal tarsus appears to be distinctive in having the following combination of features: astragalar neck relatively long and constricted, with an oblique dorsal crest and bearing a small, subspherical head; medial protuberance on the astragalar body; sulcus leading posterolaterally from the superior astragalar foramen, interrupting continuity of the lateral surface of the tibial trochlea with the groove for the flexor tendons; and well-developed contact of astragalar sustentacular and navicular facets (corresponding to a well-developed contact of sustentacular with cuboid facets on the calcaneum). Such a type, with few modifications, is present in the Pleistocene typothere *Mesotherium.*

All notoungulate tarsals from Itaboraí are extremely similar, frustrating attempts to sort them morphologically. The abundant and sole notoungulate species from the 1968 collection, *Camargomendesia pristina,* is distinct pedally in size and morphology from *Colbertia magellanica* of lot 2 when the samples are compared as a whole, but structural variations and overlapping size range (table 3) preclude identification of isolated tarsals in the common size range where both species occur. *Colbertia magellanica* is extremely variable in size (see table 2 and Paula Couto, 1952b) and may later be found to include two species (it is possible also that it is a single, sexually dimorphic species, since plots of dental and pedal measurements indicate two size peaks). Pending revision, it seems more conservative to consider the known notoungulate astragali and calcanea from Itaboraí as representing two species, *Camargomendesia pristina* and *Colbertia magellanica.* No known foot bones may be assigned confidently to the very small *Itaboraitherium atavum* because of small samples of that species, apparent broad size range in these notoungulates generally, and difficulty of distinguishing juveniles. The described and figured morphology is that referred to *Colbertia magellanica,* but is also applicable to *Camargomendesia pristina,* with differences as noted.

In dorsal profile and in depth, the astragalar body is comparable to that of *Arctocyon.* The tibial trochlea, mildly convex antero-

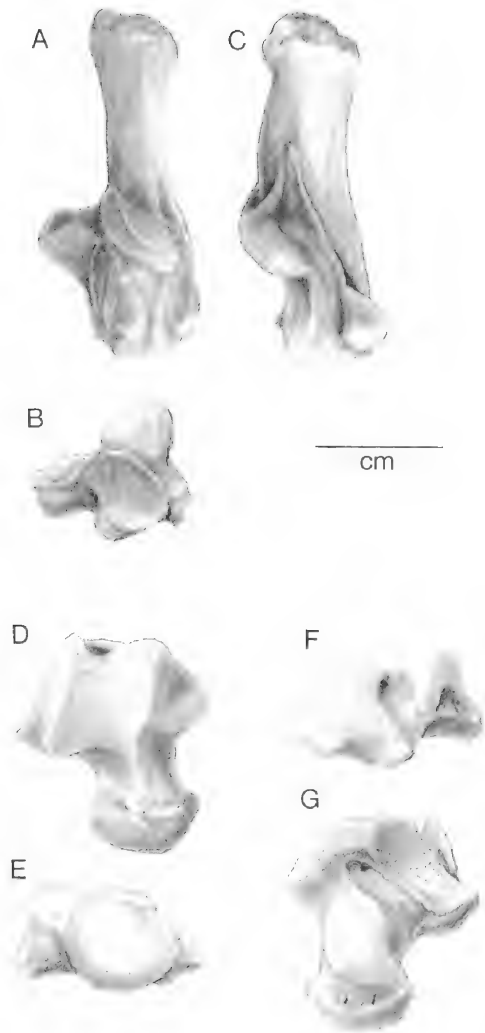

FIG. 11. Left calcaneum (DNPM LE446B) and right astragalus (AMNH 55373) of *Colbertia magellanica.* Calcaneum shown in dorsal (A), distal (B), and lateral (C) views: astragalus shown in dorsal (D), distal (E), posterior (F), and plantar (G) views. Measurements given in table 6.

posteriorly and with a shallow median concavity, presents a slight angle to the long axis of the neck; the lateral border is higher than the medial and is moderately sharp. The lateral wall of the body is vertical and bears a fibular shelf; posteriorly, the fibular facet curves dorsad and reaches to the posterior margin of the lateral tibial trochlea, subadjacent to the superior astragalar foramen. Between this foramen and the groove for the

digital flexor tendons, a sulcus courses laterally to the fibular wall of the astragalar body. This evidently housed the nerve(s) or vessel(s) which passed through the astragalar foramen, and protected them from deformation by the weight of the tibia during extreme flexion or by the flexor tendons during extreme extension (dorsiflexion) at the crurotarsal joint, and is unique to notoungulates among the groups studied. The medial border of the tibial trochlea is not sharp, and the articular surface slopes medially to a moderate extent. Inferior to this, the body projects medially to a well-marked protuberance which is approximately at the level of the middle of the tibial trochlea. This is analogous to the condition in *Tetragonostylops* and *Carodnia,* as described elsewhere, and as in those forms suggests well-developed medial short collateral ligaments, which would restrict eversive movement at the crurotarsal joint. The astragalar neck is constricted and moderately long (longer in *Camargomendesia pristina*), and bears a salient oblique crest for attachment of the astragalocalcaneal ligament. The head, relatively smaller in *C. pristina,* is more expanded dorsoventrally on its medial side but less broad transversely than in *Arctocyon,* giving it a more spherical appearance. The medial collateral ligament facet is large but not sharply distinct from the navicular facet; there is no facet for the cuboid. Articulation with appropriately sized calcanea indicates also that astragalocuboid contact would have been slight, or more probably lacking, so that the tarsus would have been functionally serial.[4] The navicular facet is strongly convex along both major and minor axes; the major axis has an orientation similar to that of *Arctocyon,* that is, oblique to the axis of the crurotarsal joint. At its lateral margin, the navicular facet is broadly continuous inferiorly with the astragalar sustentacular facet, a continuity also well shown on the calcaneum. The astragalocalcaneal facets do not appear otherwise to depart from the hypothesized primitive condition. The ectal facet is obliquely oriented, has moderate curvature and faces somewhat outward, and is separated from the sustentacular facet by a deep interarticular sulcus. The sustentacular facet occupies the inferior surface of the astragalar neck, is slightly concave along that axis, and does not continue posteriorly to the prominence marking the digital flexor groove, which is very distinct.

The calcaneum is rather similar to that of *Arctocyon.* The ectal facet is broad, gently convex, and laterally borders an obliquely oriented fibular facet. The sustentaculum, whose anterior margin is at the level of the posterior part of the cuboid facet, bears an oval facet which extends anterolaterally up the neck of the calcaneum. A protuberance, variable in development, marks the lateral termination of the sustentacular facet, and probably indicates the origin of the extensor digitorum brevis muscle and the extensor retinaculum. The cuboid facet is shallower, broader, and more obliquely oriented with respect to the long axis of the calcaneum than in *Arctocyon.* The inferior protuberance for origin of the calcaneocuboid and calcaneocuneiform ligaments is moderately developed. On the medial side of the body, a faint groove and ridge marking the course of the deep digital flexor tendon(s) is visible, just posteroinferior to the sustentaculum. The peroneal tubercle, on the fibular side of the calcaneum, is rather variable but generally moderate in development.

XENARTHRA

The only previously described xenarthran material from Itaboraí consists of four incomplete plates referred by Scillato Yané (1976) to the Dasypodidae as *Prostegotherium* aff. *astrifer* Ameghino. The earliest previously known tarsae material also pertaining to a dasypodid, *Utaetus buccatus,* derives

[4] Among primitive feet, the distinction between a "serial" and "alternating" tarsus seems to be in many cases slight and arbitrary; with isolated specimens it is often difficult to distinguish the two conditions. Early workers (e.g., Cope, 1884; Osborn, 1889), who considered the serial condition to be primitive based on its presence in *Phenacodus* (see Matthew, 1897; Simpson, 1937), employed this distinction in the erection of higher classifications. In this sense, where strongly modified higher groups of mammals are concerned, it seems to be a useful character and to reflect significant differences among adaptively similar animals, as shown by Osborn, 1889. Among ponderous, graviportal ungulates ("Amblypoda"), for instance, arsinoitheres and proboscideans have a completely serial tarsus, while that of uintatheres and astrapotheres is very strongly alternating.

from the Casamayoran of Patagonia and was described by Simpson, 1948.

There is no genral agreement as to the grouping of the major types of South American edentates (Xenarthra). Simpson (1945) followed Flower (1882) in uniting sloths and anteaters (Pilosa, *sensu lato*) to the exclusion of armadillos and allies (Cingulata), but Patterson and Pascual (1972) considered the anteaters (Vermilingua) as a separate group of equal rank to the other two, and not particularly allied with either. Comparison of astragali of representatives of each of these major groups with that of a primitive morphotype such as *Protungulatum* or *Arctocyon* indicates the cingulate tarsus to be the most primitive of these major groups (see below), and that of the Dasypodidae to be primitive within the Cingulata. As represented by the living *Dasypus novemcinctus,* the astragalar body is low, broad, and anteroposteriorly shortened; the tibial trochlea is broad and lacks the superior astragalar foramen (probably a derived condition; see below). The medial trochlear border is defined by a relatively sharp crest and the medial wall of the astragalar body is vertical; the fibular crest, also well marked but less so than the medial crest, is anteroposteriorly more elongate than the latter. The fibular wall is also vertical and a fibular shelf is variably developed among modern species. The groove for the digital flexor tendons is not distinct from the posteroinferior margin of the tibial trochlea. The astragalar neck is transversely broad but shallow; the head, also shallow, bears a single facet (navicular) which in orientation and shape is similar to that of *Arctocyon.* The sustentacular facet is relatively small and obliquely oriented with respect to the astragalar neck (probably derived); laterally it is separated by a very shallow interarticular sulcus from the ectal facet, which is deeply concave and transversely broad. Many of these features were indicated by Simpson (1931, p. 356) as characterizing the primitive xernarthran astragalus.

The variations in the pilosan (*sensu stricto*) astragalus are legion and extreme, and it is not immediately evident that megalonychid, mylodontid, or megatheriid types are derived from the primitive xenarthran type as exemplified by the Dasypodidae. However, the basic dasypodid pattern is largely preserved in the tamandua (Vermilingua), which also possesses a distinctive pilosan characteristic: the navicular facet on the astragalus, medially and inferiorly convex, laterally presents a bowl-like concavity.[5] Anteaters possess a number of other derived features in common with sloths (Flower, 1882), and if such a relationship is accepted, as it is here, common derivation from an armadilloid type is implied.

Two astragali referable to the Xenarthra are known from the DNPM Itaboraí collections. They are clearly distinct from each other, but neither can be referred confidently to a known species or genus because of a continuing lack of knowledge about early Xenarthra. It seems likely that at least one pertains to the Dasypodidae, although reference to this family is really *faut de mieux* because, as noted above, this design is considered primitive for the order. The other astragalus, possibly also dasypodid, resembles glyptodontids in certain features and is listed in that family with some doubt.

DASYPODIDAE, GENUS AND SPECIES UNDETERMINED
Figure 12

The body of this left astragalus is low, transversely broad, and anteroposteriorly shortened. A vestige of the superior astragalar foramen, filled with cancellous bone, is present posterolaterally on the tibial trochlea, which is moderately deep. As in *Utaetus,* the medial crest is not so sharply defined as in *Dasypus* or other known members of the family. Both medial and lateral walls of the astragalar body are vertical, and a small fib-

[5] This unusual feature is present also in *Manis,* whose astragalus is similar in other respects to that of *Proschizmotherium,* a megalonychid from the late Oligocene of Patagonia (among sloths, the astragalus of megalonychids appears to be the most primitive). Thus, if manids are related to the Xenarthra, as workers prior to about 1900 generally believed, then they would belong specifically with the sloths. However, as detailed further below, the astragalus of early fossil manids and palaeanodonts lacks this specialization, being armadilloid in appearance (Matthew, 1918; Simpson, 1931). Emry (1970) has argued that palaeanodonts are pholidotans and are closely related to true manids.

ular shelf protrudes from the anteroinferior angle of the lateral wall. As in cingulates generally, the neck is relatively wide, short, and shallow, and a well-defined crest occupies its dorsodistal extremity which, as in living dasypodids, would have given rise to the astragalonavicular ligament. The head is relatively narrower transversely than in *Utaetus* and living forms, but the conformation of the navicular facet is approximately the same. Unlike *Utaetus,* which is more similar to *Protungulatum* in this respect, the astragalar sustentacular facet is somewhat elongate, extending posteromedially to the angle of the astragalar body and contacting the groove for the digital flexor tendons. This groove is broad and poorly defined, not being distinct dorsally from the posterior margin of the tibial trochlea. The astragalar ectal facet is similar to known dasypodids in being broad and sharply concave, but the interarticular sulcus separating it from the sustentacular facet is slightly better developed.

?GLYPTODONTIDAE, GENUS AND SPECIES UNDETERMINED

Figure 12

This astragalus is quite distinct morphologically from the above and is also much smaller. The tibial trochlea, which lacks the superior astragalar foramen, is very deep and its lateral borders are strong and condyloid. This and the fact the medial tibial articular surface does not extend anteriorly past the middle of the astragalar body—describing a V-shape—gives the astragalus a glyptodontid appearance in dorsal aspect, similar to that of the Santacrucian *Propalaeohoplophorus.* The medial and lateral walls of the body are both vertical; anterolaterally a fibular protuberance is faintly developed, medially, the protuberance for attachment of the abductor hallucis brevis muscle and the medial collateral ligaments, found in glyptodontids, is lacking. The astragalar neck is shallow and broad transversely, but notably less so than in *Utaetus* and other known dasypodids. The ectal facet is broad and rather deeply concave, as in dasypodids and unlike the more derived condition seen in advanced glyptodontids, in which it is planar and depressed inferiorly to the level of the digital flexor groove. The sustentacular facet is similar in size and configuration to that of *Utaetus* and *Arctocyon,* not reduced as in modern *Dasypus.* The digital flexor groove is not distinct from the posteroinferior margin of the tibial trochlea.

DISCUSSION

Characters of the tarsus have been widely recognized as having phylogenetic significance since at least the time of Cope (e.g., 1884), but wide recognition does not imply wide usage. This is somewhat of an irony because most of the existing structure of ordinal and supraordinal ungulate classification dates to Cope's time, and is based largely on cheiridial morphology. Simpson's (1945) superorder Paenungulata, of particular interest here, including the orders Pantodonta, Dinocerta, Pyrotheria, Proboscidea, Embrithopoda, Hyracoidea, and Sirenia, is essentially Osborn's (1898) Amblypoda, minus the periptychid condylarths (Simpson, 1937), and including the "subungulates" generally considered to be of African origin.[6] Although a review of the Paenungulata (minus the Pantodonta, including *Deltatherium,* which appear dentally not to belong here but, with the Tillodontia, seem to represent a separate Late Cretaceous *Cimolestes*-like derivate; and minus the Hyracoidea, which may belong here but do not fit in pedally) cannot be attempted here, it is relevant to note that paenungulates, plus the Astrapotheria (including trigonostylopoids) and *Carodnia,* share a basically similar "amblypod" tarsal pattern: the astragalar body bears a low tibial trochlea with a broad anteroposterior curvature and little or no median concavity; the tibial trochlea generally extends onto the neck of the astragalus which is short and robust (or lacking entirely), and bears an expanded, flattened head; the ectal and sustentacular facets are flattened, elongate, and subparallel; and the astragalar body is expanded medially. Large, specialized members of these groups tend to have feet which confusingly resemble each

[6] These groups, and others under consideration here, were reshuffled among mammalian higher categories by McKenna, 1975, who erected the Mirorder Meridungulata to contain all of South America's native ungulates as a monophyletic unit.

other, although most can be distinguished by diagnostic contrasting specializations. In a general way, the amblypod tarsus seems to be associated with a graviportal habitus (Osborn, 1929). Functional interpretation is hampered by the near absence of living forms, but from primitive representatives of several of the groups in question (*Tetragonostylops,* Astrapotheria; *Phenacolophus,* Embrithopoda; *Mongolotherium,* Dinocerata) it seems evident that these basic modifications of the foot are not due strictly to graviportal adaptations alone, since the genera cited are relatively small, but perhaps are associated with pentadactyl digitigrady, which is shared by all amblypods in the sense enjoined here. The non-Neotropical amblypods, whether an artificial assemblage or a monophyletic group, fall into two categories characterized by different specializations of the tarsus: (1) Embrithopoda-Proboscidea; in which the calcaneofibular contact is modified and the astragalar head reduces and loses contact with the cuboid (serial tarsus), and (2) Dinocerata; in which calcaneofibular contact is lost, the medial malleolar facet of the astragalus is well developed, and the astragalocuboid contact is expanded, so that the calcaneum virtually loses its weight-bearing function (alternating tarsus). Of the South American amblypods, *Carodnia* and the Pyrotheria are similar to the first group, whereas the Astrapotheria is similar to the second.

Carodnia and its synonym, *Ctalecarodnia,* once considered a possible pyrothere (Simpson, 1945), was placed in its own order, Xenungulata, by Paula Couto, who remarked "*Carodnia* is so distinct from all the known groups of ungulates that a detailed comparative study is not necessary to disclose its affinities" (Paula Couto, 1952, p. 386). Later workers (e.g., Patterson and Pascual, 1972; Simpson, 1978) have upheld this view, which merely emphasizes the autapomorphous characters of the genus. As noted above, many advanced conditions of the ankle cited in the description are common among amblypods. It is significant, however, that astrapotherian specializations, such as the strongly developed astragalar cuboid facet, medial extension of the navicular/medial collateral ligament facets on the astragalar head, and strong anteroposteriorly extended astraglar medial malleolar facet, are lacking. *Carodnia* is not primitive but differently specialized in these respects. Comparison with *Pyrotherium,* which has one of the most derived ankles of any known amblypod, is hampered because the tarsals are not well known in that genus. The astragalus of *Pyrotherium* was mentioned and figured several times by Ameghino (e.g., 1897) and was described by Gaudry (1909) in a posthumous publication.[7] The cuboid facet, as in *Carodnia,* is lacking and the navicular facet is flat, not curving medially as in astrapotheres. There are no features which could be considered synapomorphous with notoungulates (such a special relationship was proposed by Patterson, 1977). Simpson (1935b) also noted a strong dental resemblance between *Carodnia* and the Holarctic Dinocerata, or uintatheres, and various workers have commented on a special relationship between these two groups

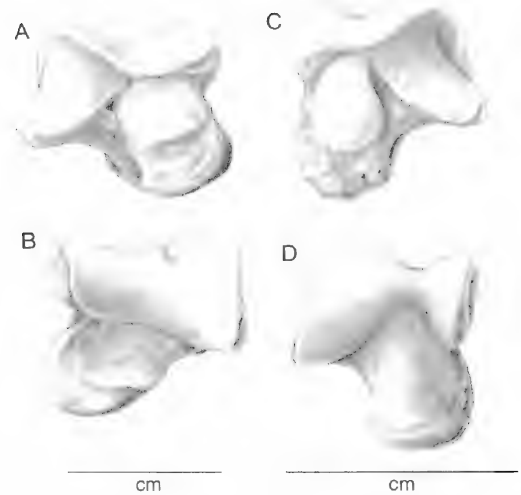

FIG. 12. Left astragalus of Dasypodidae, genus and species undetermined (DNPM LE449B; A, B) and right astragalus of ?Glyptodontidae, genus and species undetermined (DNPM LE449A; C, D) in plantar (A, C) and dorsal (B, D) views. Measurements given in table 6.

[7] The original specimen cannot now be found in the Ameghino Collection, but AMNH 11727 is a good cast of it. AMNH 11727 includes also an amorphous and enigmatic cast of a supposed calcaneum, but this specimen adds no knowledge.

(Wheeler, 1961; McKenna, 1981). Comparison of tarsals of *Carodnia* to those of a primitive uintathere such as *Mongolotherium* or *Bathyopsis* reveals the same suite of contrasting specializations as regards the astrapotheres.

Traditionally, the poorly known trigonostylopoids have been considered close allies of the Astrapotheria. However, Simpson (1967) placed the family Trigonostylopidae in a new order, Trigonostylopoidea, stating that "a common ancestor (i.e., with the astrapotheres) would almost have to be on the evolutionary level of the Condylarthra" (1967. p. 196). This view was recently challenged by Carbajal et al. (1977), based on a consideration of the Casamayoran genus *Albertogaudrya,* referred by Simpson (1967) to the Trigonostylopidae but considered by them to be an astrapotheriid.

Ameghino (1904) described and figured several isolated astragali from the Casamayoran (Notostilopense in his usage) of Patagonia as *Trigonostylops* "*minimus,*" *T. wortmani,* and the Trigonostylopidae, indet. Restudy of these specimens indicates them all to be notoungulate, that of *T. wortmani* (Ameghino, 1904, fig. 8) possibly pertaining to an isotemnid. In the same paper, Ameghino figured an astragalus he assigned to *Albertogaudrya unica.* This astragalus, noted in the original description of the family Albertogaudryidae but not of the genus (Ameghino, 1901), is contained in the genoholotype specimen, MACN 12000. Simpson (1967, p. 231) has noted that this probably was not associated with dental remains of that specimen. The astragalus is poorly preserved and enigmatic as to affinities. The tibial trochlea is low, with little curvature, and extends onto the shortened astragalar neck; a vertical medial malleolar facet is present, and what remains of the astragalocalcaneal facets indicates them to have been elongate, flat, and subparallel. This is reminiscent of astrapotheres (although more advanced in all respects than the Mustersan *Astraponotus*), but the head seems to have lacked the cuboid facet,[8] which is prominent in *Tetragonostylops* and astrapotheres but lacking in *Carodnia* and *Pyrotherium.* It is possible that the specimen belongs to the Casamayoran pyrothere, *Carolozittelia.*

The proximal part of the ankle is known in *Parastrapotherium* and *Astrapotherium* (Scott, 1937), and isolated astragali from the Mustersan may be referred to *Astraponotus* with little doubt. In all forms, as in *Tetragonostylops,* the medial malleolar facet is well developed and medially expanded, possibly assuming a weight-bearing function; the astragalocuboid contact is expanded and the navicular facet extends medially; the calcaneal peroneal tubercle (unknown in *Astraponotus*) is enlarged and calcaneofibular contact is lacking (unlike the condition in *Tetragonostylops*). Because Deseadan and later astrapotheres are gigantic, strongly modified graviportal forms, comparison of *Tetragonostylops* with *Astraponotus* is instructive. In the latter genus, the astragalar fibular shelf and medial collateral ligament facets (primitive characters) lacking in later astrapotheres are present and, significantly, the unusual secondary astragalar ectal facet (for articulation with the dorsal astragalar neck) is present. This and the derived features noted above strongly suggest that the Itaboraí species, and by implication the family Trigonostylopidae, is closely related to the Astrapotheria. In many respects, *Tetragonostylops* is pedally more primitive than later astrapotheres, and in others (e.g., the enormously developed peroneal shelf), it is clearly autapomorphous. As noted above, the Astrapotheria present tarsal specializations similar to those of the Dinocerata although in one feature, loss of calcaneofibular contact, this seems to be convergent (such a contact is present in *Tetragonostylops*). If the paenungulates, in the sense enjoined here represent a monophyletic group, then two major clades are suggested: Astrapotheria-Dinocerata and Pyrotheria (including *Carodnia*)-Proboscidea-Embrithopoda. This is, however, frankly speculative at this juncture, since it is only the vague "amblypod" tarsal features cited above, coupled with generalized trends (such as graviportal adaptation and gigantism) which unites this assemblage.

The South American condylarths and li-

[8] This cannot be determined with certainty, since some of the astragalar head is missing.

topterns have long been considered closely related: Scott, 1913, grouped the Didolodontidae ("Didolodidae") within the Litopterna, and Simpson (1948, p. 119) stated that "the litopterns appear to represent the direct further evolution of the Condylarthra, continuing in South America after they became extinct in the rest of the world." Because most of the described species from the early Tertiary are known only by isolated teeth, it is difficult to make extensive comparisons and erect dental diagnoses separating these two groups. A reevaluation of the interrelationships of these early forms is deferred, pending completion of work in progress. It is evident, however, that the problem of distinguishing litopterns from didolodonts is intensified by the discovery that *Ernestokokenia parayirunhor* and a new undescribed form, dentally among the most primitive of all known eutherians from South America, bear the unmistakable litoptern ankle specializations, whereas other didolodonts (including a supposed congener of *Ernestokokenia parayirunhor, E. protocenica*) and a dental litoptern, *Victorlemoinea prototypica,* do not. This suggests that, as in artiodactyls (Schaeffer, 1948), the primary specializations of the Litopterna were pedal not dental. These specializations, including modifications for strictly orthal joint movement and for rapid flexion of the crurotarsal joint, as seen in the relatively posterior position of the astragalocalcaneal facets on the calcaenum, plus the very small body size also suggest that the most primitive litopterns may have been saltatory rather than cursorial in their mode of locomotion. Perhaps these adaptations, which are similar in many respects for the two locomotor modes, were in a sense preadaptive to the later radiations of large, cursorial litopterns.

The Itaboraí litoptern tarsals, pertaining to *Anisolambda prodromus, Ernestokokenia parayirunhor,* and the unnamed form, are closely similar and resemble most those ascribed to *Protheosodon coniferus* by Loomis, 1914 (see comments, table 1). The Santa Cruz proterotheres and macraucheniids have, respectively, distinct ankles which may both be derived from this primitive pattern.

Victorlemoinea, considered by Simpson (1948) to be a member of the Macraucheniidae, probably lacked the litoptern specializations of the tarsus, although this will not be certain until an articulated skeleton is found. Dentally, there are some molar specializations (e.g., posthypocone cingulum-hypocone-metaconule crest in the upper molars) of *Victorlemoinea* suggestive of the Macraucheniidae, but the genus is aberrantly specialized in some respects and far more derived than the most primitive undoubted members of the family, the Cramaucheniinae, which are known primarily from the Colhuehuapian (Soria, 1981) and Santacrucian (Scott, 1910) but also by a few specimens in the Deseadan. It seems likely that *Victorlemoinea* is not a litoptern, but a precociously specialized relative that was convergent upon them. Its only clear relative is *Phoradiadus* (Simpson, Minoprio, and Patterson, 1962) from the peculiar Divisadero Largo (?early Deseadan) fauna from near Mendoza, Argentina (Soria, 1981, and personal observ.). Possibly both are referable to the Sparnotheriodontidae, which is based on a litoptern-like mandible, of very advanced aspect, from the Casamayoran of Patagonia (Soria, 1980).

Tarsals of ?*Victorlemoinea prototypica* and the remaining condylarth-like species, *Ernestokokenia protocenica* and ?*Lamegoia conodonta,* seem to form a natural group when compared to other South American forms and with various North American condylarths. In all of them, the nearly vertical facet for the medial malleolus of the tibia is well developed and expanded anteriorly, extending well onto the neck of the astragalus, and the calcaneal cuboid facet is dorsally expanded into a prominent beak. These features are not known among the litopterns, but the litoptern tarsus is so modified that it is difficult to say with conviction that such characters were not present in a common ancestor of the two groups. *Ernestokokenia protocenica* and ?*Lamegoia conodonta* are especially alike in a number of derived similarities: the peroneal tubercle of the calcaneum extends posterodorsally to terminate at the base of the ectal protuberance, the astragalar head is medially and transversely expanded and lacks a medial collateral ligament facet and cuboid contact, the astragalar tibial trochlea is deepened, and the anterior part of the medial malleolar facet flares sharply mediad. A

similar astragalus, tentatively assigned to *Didolodus,* is known from the Casamayoran of Patagonia. These tarsals also lack the presumably autapomorphous features of ?*Victorlemoinea,* such as the anteroposteriorly expanded sustentacular facet (with a corresponding facet on the calcaneum), thickened calcaneal sustentaculum, and a large rugose peroneal tubercle.

The primitive members of the great order Notoungulata possessed a rather generalized tarsus, although the combination of derived astragalocalcaneal conditions noted above are distinctive and do make isolated tarsals readily recognizable. *Colbertia magellanica* is currently placed in the Oldfieldthomasiidae (Paula Couto, 1952b) which, as generally conceived, is a wastebasket family including generally primitive typotherian (including both typotheres and hegetotheres) notoungulates above the notioprogonian grade (Simpson, 1948). Because of the absence of typically typotherian specializations (cristid obliqua of lower molars with a narrow anterior attachment to the metalophid: upper molars with crochet and second crista joined, first crista joined to the protoloph directly or by an antecrochet), *Colbertia* and some of the other oldfieldthomasiids, such as *Maxschlosseria, Brachystephanos,* and *Xenostephanos* might with equal validity be placed in the Isotemnidae. Simpson (1967) indicated the accessory trigonid cuspule, which I interpret as a paraconid, to be one of the distinguishing features of isotemnids and it is found in the genera listed, but it has a still wider distribution and is probably primitive for the Notoungulata as a whole. The tarsus of *Colbertia* does not differ greatly from that of *Camargomendesia pristina,* which pertains to a truly primitive family, the Henricosborniidae (Paula Couto, 1978c, 1979; see Simpson, 1948, and Pascual, Vucetich, and Fernandez, 1978) or from that of *Boreastylops* (Notostylopidae), ?*Pleurostylodon* (Isotemnidae), or *Trachytherus* (Mesotheriidae). This broad distribution among the major groups of Notoungulata indicates that it is a generalized pattern for the order. Various notoungulate families, including the Homalodotheriidae, Leontiniidae, Notohippidae, and the Toxodontidae among the Toxodonta and the Interatheriidae (see Stirton, 1953) and the Hegetotheriidae among the Typotheria may be characterized and grouped by tarsal specializations away from this generalized type.

As with the litopterns and South American condylarths, there seems to be no North American ungulate which presents pedal specializations strongly indicative of notoungulate relationships. The tarsus of the supposed Holarctic notoungulates, the Arctostylopidae, is unknown. The most comparable North American ungulate tarsals pertain to the Hyopsodontidae. In *Promioclaenus aequidens,* AMNH 823, the calcaneal sustentacular facet extends anteriorly to achieve broad contact with the cuboid facet, the astragalar body has a median projection (also true of *Hyopsodus walcottianus,* AMNH 14654), and the lateral side of the tibial trochlea is interrupted posteriorly by a sulcus extending laterally from the superior astragalar foramen (possibly but not surely also true of *H. walcottianus*). These derived features are characteristic of notoungulates, but the auditory region of *Hyopsodus* (Cifelli, 1982) is far more primitive than that of any known notoungulate (see Patterson, 1934; Simpson, 1948, and Pascual, Vucetich, and Fernandez, 1978).

The two known xenarthran astragali from Itaboraí are distinct from each other and surely represent different genera and probably families. Both are assigned to the Cingulata, although as noted this is based on the absence of typical derived pilosan characters rather than the presence of distinctively cingulate features. The strongly constricted tibial trochlea of DNPM LE449a, with salient, condyloid, medial and lateral crests is (are) derived condition(s) similar to glyptodontids, suggesting that this family may have been distinct, at least pedally, by the Riochican; this specimen does, however, lack other distinctive and presumably later derived features of the glyptodont tarsus, such as a flattened sustentacular facet. The other astragalus is generally similar to that of *Utaetus,* but differs from that genus and other dasypodids in the (vestigial) presence of the superior astragalar foramen. It is curious that dasypodid plates, generally such a conspicuous element of South American mammal faunas, are entirely lacking in the extensive DNPM Itaboraí collections, whereas a cur-

sory survey revealed astragali of two cingulate types as well as a number of other postcranial remains. Considering the condition of the bone and the abundant herpetofauna, it is highly unlikely that this is an artifact of collecting or preservational bias.

Matthew and Granger (1918), following a suggestion by Osborn (1904), placed their then new North American suborder Palaeanodonta in the Edentata, suggesting a close relationship to both xenarthrans and pholidotans but perhaps closer to the latter. In a more extensive study, Simpson (1931) indicated palaeanodonts to be closer to the Xenarthra. This arrangement, which he followed in 1945, was widely accepted until Emry (1970) presented detailed comparisons arguing that palaeanodonts be referred to the Pholidota and that "there are no features of either the palaeanodonts or xenarthrans to indicate that they are more closely related to each other than either is to the Insectivora" (Emry, 1970, p. 503). This statement is based in part on Emry's unwarranted assumption that any similarities between the two groups are *necessarily* convergent because palaeanodonts were contemporaneous with far more derived true xenarthrans, and may be incorrect. Possession of a more primitive condition by the palaeanodonts does not exclude that condition from being synapomorphous with xenarthrans and/or pholidotans, through a common ancestor. Comparison must be made to other mammals to determine the primitiveness of the character within the Eutheria in general. As Emry observed, many of the palaeanodont-xenarthran similarities noted by Simpson (1931) seem to be primitive; this applies also to a number of palaeanodont-pholidotan similarities, from the same list, discussed by Emry. Such equivocal characters, or those for which morphocline polarity is unclear, include (2) proportions of the skull; (3) distribution of cranial foramina; (5) auditory region; (6) brain; (8), cervical vertebrae; ?(9) dorsolumbar vertebrae; (10) sacrum; (14) radius and ulna; (15) carpus; (18) femur; (19) crus; and (20) astragalus (numbers in parentheses are those used by Simpson, 1931, p. 368ff; Emry, 1970, p. 488ff). Palaeanodonts do appear to resemble manids but not xenarthrans, however, in several specialized characters, such as (1) mode of tooth reduction; (11) broad, flat transverse processes on the caudal vertebrae, and (13) distally elongated, medially turned pectoral crest on the humerus. On this basis the two groups may be tentatively allied. Possible contradictions to this arrangement include palaeanodont-xenarthran resemblances in the scapula (12; secondary scapular spine, coracoscapular notch) and dorsolumbar vertebrae (9; deepened notches for nerve exits). Derived similarities of the Pholidota/Palaeanodonta and Xenarthra with respect to other mammals, dismissed by Emry but possibly evidence of a common unique ancestor within the Eutheria are mostly features functionally related to the eating of colonial insects and powerful development of the limbs: general reduction and simplification of the dentition, mandible, and mandibular glenoid; proportions of the limbs, digits, and claws; everted and strongly crested ilia, and contact of the ischium with caudal vertebrae.

The evidence afforded by the proximal tarsals is equivocal, partially because of uncertain association of skeletal materials. Simpson (1931, p. 356) noted that, whereas the astragalus of *Metacheiromys* is distinctively xenarthran in appearance, that of *Palaeanodon* is more primitive. Emry (1970, p. 500), however, considered astragali of these two genera to be virtually identical and equally "armadilloid." In fact, there are two distinct astragalar types among specimens currently assigned to *Palaeanodon*; the narrow-bodied morph, exemplified by AMNH 15137 (Matthew and Granger, 1918, fig. 67), and the *Metacheiromys*-like morph, exemplified by AMNH 14733. It can be argued that the latter exhibits a number of derived xenarthran features—most importantly a concave astragalar ectal facet, anteroposteriorly short but transversely wide body with a strongly curved, deep tibial trochlea, and loss of a distinct groove for the digital flexor tendons—the former, however, is far more primitive and is vaguely xenarthran only in the somewhat shortened neck and transversely narrowed head. Since the more primitive astragalus is associated with partial skeletons including the type and a paratype of *Palaeanodon ignavus,* I assume that it pertains to that species and the more *Metacheiromys*-like astragali (all from another locality) perhaps be-

long to an early, unrecognized species of the latter genus. Thus, either *Metacheiromys* is more closely related to the Xenarthra than is *Palaeanodon,* or both belong to a group in which the astragalus independently converged on the hypothesized primitive xenarthran condition. Numerous derived conditions shared by these genera, described in detail by Matthew and Granger (1918) and Simpson (1931) make this hypothesis the more probable.

The situation is complicated further by consideration of the pholidotan ankle. As noted above, the astragalus of *Manis* resembles that of primitive (e.g., megalonychid) sloths, particularly in the peculiar concavo-convex astragalonavicular articulation. If the association of Miocene tarsals from Germany (described by Helbing, 1938) to *Necromanis* Filhol, 1884 (=*Teutomanis* Ameghino, 1905) is correct (Emry, 1970), then these pilosan-manid similarities were almost surely acquired independently. *Necromanis* appears to lack the astragalar pivot (but see Szalay, 1977, p. 349) and is more primitive in certain respects (presence of a prominent superior astragalar foramen posteriorly dividing the tibial trochlea, astragalar body not transversely expanded and with a median projection) than the palaeanodont-*Manis* assemblage considered as a whole. An astragalus nearly identical with that of *Necromanis* is known from a partial ?pholidotan skeleton from the Ulan Gochu beds of the Shara Murun region, Mongolia.

Mention should be made of several recent discoveries of possible non-South American xenarthrans, although the ankle is not well known in these forms. *Ernanodon antelios,* from the ?late Paleocene of Guangdong, south China, has been implicated as a primitive edentate (Ding, 1979). The posterior dorsal vertebrae are described as showing "incipient" xenarthrous articulations, but they are not unambiguously xenarthrous, and similarly incipient types are found among other mammals such as didelphids and palaeanodonts. The ischium of *Ernanodon* may have contacted but probably did not fuse with the caudal vertebrae; the skeleton is otherwise remarkably primitive, but the manid-like pectoral crest of the humerus and general "edentate" trend of the dentition suggest that it is possibly a primitive member of the palaeanodont-pholidotan complex.

Storch (1981) has described a remarkably complete skeleton from the middle Eocene of Germany as *Eurotamandua joresi,* referring it to the Myrmecophagidae. The specimen is strikingly anteater-like, but as figured seems to lack a number of myrmecophagid, pilosan, and xenarthran characters (see Engelmann, 1978). The posterior dorsal and anterior lumbar vertebrae (Storch, 1981, fig. 8) each have posteriorly extended transverse processes, contacting the centrum of the following vertebrae. This is an uncommon (although not unparalleled) condition among mammals, but is rather unlike the condition in the South American edentates. In those forms, the postzygapophysis is completely locked between the prezygapophysis and transverse process of the preceding vertebra. Ischiocaudal contact seems to be present in *Eurotamandua* (Storch, 1981, fig. 7), but it does not appear to differ significantly from the condition in *Manis.* As in Xenarthra (and many other mammals) a secondary scapular spine is present and teeth are lacking, as in anteaters. The astragalus is not well shown, but of other details in which pilosans are specialized, *Eurotamandua* lacks the scapular fenestra and reduction of the zygomatic arch. The complete lack of teeth is a similarity to vermilinguans, but the muzzle is not clearly so elongate nor are the ribs flattened and overlapping as in the South American forms. Perhaps *Eurotamandua* also pertains to the pholidotan-palaeanodont assemblage which, together with the aberrant and poorly understood epoicotheres, may represent a significant but hitherto largely undocumented radiation of North American-Old World edentates. The balance of evidence presented above suggests that, in essential agreement with Matthew (Matthew and Granger, 1918), these forms together with the Xenarthra may form a remotely related but monophyletic group of primitive Eutheria.

LITERATURE CITED

Ameghino, F.
1897. Les mammifères crétacés de l'Argentine. Deuxième contribution à la con-

naissance de la faune mammalogique des couches à *Pyrotherium*. Bol. Inst. Geogr. Argentina, vol. 18, pp. 406–521.
1901. Notices préliminaires sur les ongulés nouveaux dés terrains crétacés de Patagonie. Bol. Acad. Nac. Cien. Cordoba, vol. 16, pp. 349–429.
1904. La perforación astragaliana en los mamíferos no es un caracter originariamente primitivo. An. Mus. Nac. Buenos Aires, ser. 3, vol. 4, pp. 349–460.

Camp, C. L., and N. Smith
1942. Phylogeny and function of the digital ligaments of the horse. Mem. Univ. California, Berkeley, vol. 13, pp. 69–124.

Carbajal, E., R. Pascual, R. Pinedo, J. A. Salfity, and M. G. Vucetich
1977. Un nuevo mamífero de la Formación Lumbrera (Grupo Salta) de la Comarca de Carahuasi (Salta, Argentina). Edad y correlaciones. Publ. Mus. Munic. Cien. Natur. Mar del Plata "Lorenzo Scaglia," vol. 2, pp. 148–163.

Chaplin, R. E.
1971. The Study of Animal Bones from Archaeological Sites. London, Seminar Press, pp. 1–170.

Cifelli, R. L.
1982. The petrosal structure of *Hyopsodus* with respect to that of some other ungulates, and its phylogenetic implications. Jour. Paleontology, vol. 56, pp. 795–805.

Cope, E. D.
1884. The Vertebrata of the Tertiary formations of the west. Repts. U.S. Geol. Survey Territ., vol. 3, pp. 1–1003.

Ding, S.
1979. A new edentate from the Paleocene of Guangdong. Vert. Palasiatica, vol. 17, pp. 57–64.

Emry, R. J.
1970. A North American Oligocene pangolin and other additions to the Pholidota. Bull. Amer. Mus. Nat. Hist., vol. 142, pp. 455–510.

Engelmann, G. F.
1978. The logic of phylogenetic analysis and the phylogeny of the Xenarthra (Mammalia). Ph.D. dissertation, Columbia Univ.

Flower, W. H.
1882. On the mutual affinities of the animals composing the Order Edentata. Proc. Zool. Soc. London, pp. 358–367.

Francisco, B. H. R., and F. L. de Souza Cunha
1978. Geologia e estratigrafia de bacia de São Jose, Municipio de Itaboraí, RJ. An. Acad. Brasil. Cien., vol. 50, pp. 381–416.

Gaudry, A.
1909. Fossiles de Patagonie: Le *Pyrotherium*. An. Paléontol. (Paris), vol. 4, pp. 1–28.

Gingerich, P. D.
1977. Correlation of tooth size and body size in living hominoid primates, with a note on relative brain size in *Aegyptopithecus* and *Proconsul*. Amer. Jour. Phys. Anthrop., vol. 47, pp. 395–398.

Grambast, L., L. Martinez, M. Mattauer, and L. Thaler
1967. *Perutherium altiplanense*, nov. gen., nov. sp., premier mammifère mésozoique d'Amerique du Sud. C.R. Acad. Sci., sér. D, vol. 264, pp. 707–710.

Helbing, H.
1938. Nachweis manisartiger Säugetiere im stratifizierten europäischen Oligocaen. Eclog. Geol. Helvetiae, vol. 31, pp. 293–303.

Kay, R. F.
1975. The functional adaptations of primate molar teeth. Amer. Jour. Phys. Anthrop., vol. 43, pp. 195–216.

Kielan-Jaworowska, Z.
1977. Evolution of therian mammals in the Late Cretaceous of Asia. Part II. Postcranial skeleton in *Kennalestes* and *Asioryctes*. Palaeontol. Polon., vol. 37, pp. 65–83.

Loomis, F. B.
1914. The Deseado Formation of Patagonia. Concord, The Rumford Press, pp. 1–232.

McKenna, M. C.
1956. Survival of primitive notoungulates and condylarths into the Miocene of Colombia. Amer. Jour. Sci., vol. 254, pp. 736–743.
1975. Toward a phylogenetic classification of the Mammalia. *In* Luckett, W. P., and F. S. Szalay, eds., Phylogeny of the Primates. New York, Plenum Press, pp. 21–46.
1981. Early History and biogeography of South America's extinct land mammals. *In* Ciochon, R. L., and A. B. Chiarelli, eds., Evolutionary Biology of the New World Monkeys and Continental Drift. New York, Plenum Press, pp. 43–77.

Marshall, L. G.
1978. Evolution of the Borhyaenidae, extinct South American predaceous marsupials. Univ. California Publ. Geol. Sci., vol. 117, pp. 1–89.

Marshall, L. G., R. Pascual, G. Curtis, and R. Drake
1977. South American geochronology; radiometric time scale for middle to late Tertiary mammal bearing horizons in Patagonia. Science, vol. 195, pp. 1325–1328.

Marshall, L. G., R. Hoffstetter, and R. Pascual
[In press] Geochronology of the continental mammal bearing Tertiary of South America. *In* Woodburne, M. O., ed., Paleontology as a Discipline in Geochronology.

Matthew, W. D.
1897. A revision of the Puerco fauna. Bull. Amer. Mus. Nat. Hist., vol. 9, pp. 59–110.
1937. Paleocene faunas of the San Juan Basin, New Mexico. Trans. Amer. Phil. Soc., new series, vol. 30, pp. 1–510.

Matthew, W. D., and W. Granger
1918. A revision of the lower Eocene Wasatch and Wind River faunas. Part 5. Insectivora (continued), Glires, Edentata. Bull. Amer. Mus. Nat. Hist., vol. 34, pp. 429–483.

Novacek, M. J.
1980. Cranioskeletal features in tupaiids and selected Eutheria as phylogenetic evidence. *In* Luckett, W. P., ed., Comparative Biology and Evolutionary Relationships of Tree Shrews. New York, Plenum Press, pp. 35–93.

Osborn, H. F.
1889. The Mammalia of the Uinta Formation. Part IV. The evolution of the ungulate foot. Trans. Amer. Phil. Soc., new series, vol. 16, pp. 530–569.
1898. Evolution of the Amblypoda. Part I. Taligrada and Pantodonta. Bull. Amer. Mus. Nat. Hist., vol. 10, pp. 169–218.
1904. An armadillo from the middle Eocene (Bridger) of North America. *Ibid.*, vol. 20, pp. 163–165.
1929. The titanotheres of ancient Wyoming, Dakota, and Nebraska. U.S. Geol. Surv. Monograph 55 (2 vols.), pp. 1–953.

Pascual, R., M. G. Vucetich, and J. Fernandez
1978. Los primeros mamíferos (Notoungulata, Henricosborniidae) de la Formación Mealla (Grupo Salta, Subgrupo Santa Barbara). Sus implicancias filogenéticas, taxonómicas, y cronológicas. Ameghiniana, vol. 15, pp. 366–390.

Patterson, B.
1936. The internal structure of the ear in some notoungulates. Geol. Ser. Field Mus. Nat. Hist., vol. 6, pp. 199–227.
1977. A primitive pyrothere (Mammalia, Notoungulata) from the early Tertiary of northwestern Venezuela. Fieldiana (Geol.), vol 33, pp. 397–422.

Patterson, B., and R. Pascual
1972. The fossil mammal fauna of South America. *In* Keast, A., F. C. Erk, and B. Glass, eds., Evolution, Mammals, and Southern Continents. Abany, State Univ. New York Press, pp. 247–309.

Paula Couto, C. de
1952a. Fossil mammals from the beginning of the Cenozoic in Brazil. Condylarthra, Litopterna, Xenungulata, and Astrapotheria. Bull. Amer. Mus. Nat. Hist., vol. 99, pp. 355–394.
1952b. Fossil mammals from the beginning of the Cenozoic in Brazil. Notoungulata. Amer. Mus. Novitates, no. 1568, pp. 1–16.
1952c. Fossil mammals from the beginning of the Cenozoic in Brazil. Marsupialia: Polydolopidae and Borhyaenidae. *Ibid.*, no. 1559. pp. 1–27.
1952d. Fossil mammals from the beginning of the Cenozoic in Brazil. Marsupialia: Didelphidae. *Ibid.*, no. 1567, pp. 1–26.
1954. On a notostylopid from the Paleocene of Itaboraí, Brazil. *Ibid.*, no. 1693, pp. 1–5.
1961. Marsupiais fósseis do Paleoceno do Brasil. An. Acad. Brasil. Cien., vol. 33, pp. 321–333.
1962. Didelfídeos fósiles del Paleoceno de Brasil. Rev. Mus. Argentino Cien. Natur. "Bernardino Rivadavia" Zool., vol. 8, pp. 135–166.
1963. Um Trigonostylopidae do Paleoceno do Brasil. An. Acad. Brasil. Cien., vol. 35, pp. 339–351.
1970. Novo notoungulado no Riochiquense de Itaboraí. Iheringia, vol. 3, pp. 77–86.
1978a. Ungulados fósseis do Riochiquense de Itaboraí, RJ, Brasil. I—Xenungulata. An. Acad. Brasil. Cien., vol. 50, pp. 203–207.
1978b. Ungulados fósseis do Riochiquense de Itaboraí, RJ, Brasil. II—Condylarthra e Litopterna. *Ibid.*, vol. 50, pp. 209–218.
1978c. Ungulados fósseis do Riochiquense de Itaboraí, RJ, Brasil. III—Notoungulata, Trigonostylopoidea. *Ibid.*, vol. 50, pp. 219–226.
1979. Ungulados fósseis do Riochiquense de Itaboraí, RJ, Brasil. IV—Ratificação sobre os Notoungulata. *Ibid.*, vol. 51, pp. 345–348.

Schaeffer, B.
1947. Notes on the origin and function of the artiodactyl tarsus. Amer. Mus. Novitates, no. 1356, pp. 1–24.
1948. The origin of a mammalian ordinal character. Evolution, vol. 2, pp. 164–175.

Scillato Yané, G. J.
1976. Sobre un Dasypodidae (Mammalia, Xenarthra) de Edad Riochiquense (Paleoceno superior) de Itaboraí, Brasil. An. Acad. Brasil. Cien., vol. 48, pp. 527–530.

Scott, W. B.
1910. The Litopterna of the Santa Cruz beds. Repts. Princeton Univ. Expeditions Patagonia, vol. VII (Palaeontol. IV), pp. 1–156.
1913. A History of Land Mammals in the Western Hemisphere. New York, Macmillan Co., pp. 1–693.
1937. The Astrapotheria. Proc. Amer. Phil. Soc., vol. 77, pp. 309–393.

Simpson, G. G.
1931. *Metacheiromys* and the Edentata. Bull. Amer. Mus. Nat. Hist., vol. 59, pp. 295–381.
1935a. Occurrence and relationships of the Río Chico fauna of Patagonia. Amer. Mus. Novitates, no. 818, pp. 1–21.
1935b. Descriptions of the oldest known South American mammals, from the Río Chico Formation. *Ibid.*, no. 793, pp. 1–25.
1936. Skeletal remains and restoration of Eocene Entelonychia from Patagonia. *Ibid.*, no. 826, pp. 1–12.
1937. The Fort Union of the Crazy Mountain Field, Montana, and its mammalian faunas. Bull. U.S. Natl. Mus., vol. 169, pp. 1–287.
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. 1–350.
1948. The beginning of the Age of Mammals in South America. Part 1. *Ibid.*, vol. 91, pp. 1–232.
1967. The beginning of the Age of Mammals in South America. Part 2. *Ibid.*, vol. 137, pp. 1–259.
1978. Early mammals in South America: fact, controversy, and mystery. Proc. Amer. Phil. Soc., vol. 122, pp. 318–328.

Simpson, G. G., J. L. Minoprio, and B. Patterson
1962. The mammalian fauna of the Divisadero Largo Formation, Mendoza, Argentina. Bull. Mus. Comp. Zool., vol. 127, pp. 239–293.

Soria, M. F.
1980. Una nueva y problematica forma de ungulado del Casamayorense. Actas II Congr. Argentina Paleontol. Bioestrat., vol. 2, pp. 193–203.
1981. Los Litopterna del Colhuehuapense (Oligoceno tardio) de la Argentina. Rev. Mus. Argentino Cien. Natur. "Bernardino Rivadavia," vol. 3, pp. 1–54.

Stirton, R. A.
1953. A new genus of interatheres from the Miocene of Colombia. Univ. California Publ. Geol. Sci., vol. 29, pp. 265–349.

Storch, G.
1981. *Eurotamandua joresi,* ein Myrmecophagidae aus dem Eozän der "Grube Messel" bei Darmstadt (Mammalia, Xenarthra). Senckenbergiana Lethaea, vol. 61, pp. 247–289.

Szalay, F. S.
1977. Phylogenetic relationships and a classification of eutherian mammals. *In* Hecht, M. K., P. C. Goody, and B. M. Hecht, eds., Major Patterns in Vertebrate Evolution. New York, Plenum Press, pp. 315–374.

Szalay, F. S., and R. L. Decker
1974. Origin, evolution, and function of the tarsus in Late Cretaceous eutherians and Paleocene primates. *In* Jenkins, F. A. Jr., ed., Primate Locomotion. New York, Academic Press, pp. 223–259.

Vucetich, M. G.
1980. Un nuevo Notostylopidae (Mammalia, Notoungulata) proveniente de la Formación Lumbrera (Grupo Salta) del noroeste Argentino. Ameghiniana, vol. 17, pp. 363–372.

Wheeler, W. H.
1961. Revision of the uintatheres. Bull. Peabody Mus. Nat. Hist., vol. 14, pp. 1–93.